# Chemistry of Plant Phosphorus Compounds

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Arlen W. Frank

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# About the Author

Born Nov 22, 1928, in Lima, Peru; married May 24, 1958, in Galena, MD, Marcia D. Craddock; three children, eight grandchildren.

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Publications

*Books*: Frank, Arlen W., "The Cotton Gazetteer," self-published, © 1985, xii + 193 pp.; Frank, W. A. [*sic*], "Phosphonous Acids (Thio-, Seleno- Analogs) and Derivatives," Chapter 10 in Kosolapoff, G. M.; Maier, L. "Organic Phosphorus Compounds," Wiley-Interscience, New York, 1972, Vol. 4 (of 7), 531 pp.

*Reviews*: Frank, Arlen W., "The Phosphonous Acids and Their Derivatives," *Chem. Rev.* 1961, 30(4), 389–424; Frank, Arlen W., "Synthesis and Properties of N-, O- and S- Phospho Derivatives of Amino Acids, Peptides, and Proteins," *Crit. Rev. Biochem. Molec. Biol.* 1984, 16(1), 51–101.

*Other Publications*: About 50 articles and about 25 patents, mostly in the field of organophosphorus chemistry.

# Preface

This book had its inception in 1990 when I was beginning a 2-year tour of duty as a technical editor for the Gmelin Institute in Frankfurt am Main, Germany, one of the institutes of the Max Planck Society. The multivolume *GMELIN Handbook of Inorganic Chemistry* series, published by Springer-Verlag since 1924, was published in German during its early years but increasingly in English in recent years. Our task as editors was to render manuscripts written by authors not fully versed in the English language into a form suitable for publication. The presence of the joint Gmelin/Beilstein Library onsite and the University of Frankfurt's Senckenberg Library a short distance away prompted me to start work on a long-cherished dream—a comprehensive book on the chemistry of phosphorus compounds in plants—during periods of inactivity between editorial assignments. Alas, the *Handbook* ceased publication in 1998 and the Gmelin Institute itself was closed in 1999, a victim of budget constraints following the merger of the former East German Science Institutes into the Max Planck Society in the early 1990s.

My original intent was to cover all types of phosphorus compounds found in plants, both organic and inorganic, but I soon realized that some measures would have to be taken to keep the book a manageable size. The first to go were the nucleic acids RNA and DNA, despite their importance—they comprise, for example, 11.1% and 1.44%, respectively, of the total phosphorus in the duckweed *Spirodela oligorrhiza* (pp 442–443). Next to go were the inorganic phosphates—phosphoric acid ($P_i$), di- or pyrophosphoric acid ($PP_i$), and the polyphosphoric acids—70.7%, 0.17%, and undetected,[a] respectively, in *S. oligorrhiza*. Phosphoric acid presents a problem because it is difficult (but not impossible) to distinguish $P_i$ released during workup from $P_i$ already present in the plant. Last to go were the phosphoproteins because the information on them is too old and sparse to be relevant. The coverage in this book is therefore restricted to monomeric phosphorus-containing compounds with the sole exception of the starch phosphates.

A substantial setback occurred on August 29, 2005 when hurricane Katrina, with a single violent surge of flood water, destroyed all of the reprints I had assembled over the years along with most of my notes.

Little did I know that this book would take 20 years to complete, but here it is at last, my *magnum opus*.

Slidell, LA, USA
July 7, 2012

[a]The lower plants store phosphorus in the form of polyphosphates but the higher plants use phytic acid (Chapter 2) for this function.[1]

# Acknowledgments

I am grateful to the librarians and their staff of the Earl K. Long Library at the University of New Orleans and the Howard-Tilton Library at Tulane University, New Orleans, where most of my research for this book was carried out; to the editors and staff of Elsevier, in particular to Mr. Adrian Shell, Ph.D., Senior Acquisitions Editor, Oxford, UK, to Jessica Vaughan, Editorial Project Manager, Waltham, MA, and to my two Production Managers in Gurgaon, India,* Mr. Hemachander Timiri Sundaram and his staff and Mr. Mohana Priyan Rajendran and his staff, for carrying the project through to completion.

# Introduction

Arlen W. Frank

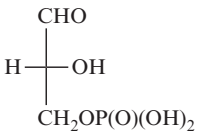
This book is intended to be a reference source for scientists engaged in any aspect of plant research—chemistry, biochemistry, or physiology—with primary focus on the chemistry of phosphorus-containing compounds that occur naturally in the plant kingdom and specifically in the higher plants (Plantae). Algae, fungi, and other lower plant forms are not covered.

In general, the subject matter is treated in order of increasing complexity, compounds of C, H, and O in Chapters 1–3 and compounds of C, H, O, and N in Chapters 4–7. Chapter 8 covers the various methods developed in early studies to determine the overall distribution of phosphorus-containing compounds in plants. Appendix A covers the changes in phosphorus-containing compounds during germination and Appendix B their accumulation during growth and senescence. The final sections of the book comprise a comprehensive list of references and a combined index of the plants and phosphorus compounds.

## The Phosphorus Compounds

### Nomenclature

The naming of the phosphorus compounds in this book conforms to the recommendations of the Drake Committee on the Nomenclature of Organic Phosphorus Compounds published in 1952.[2] *Chemical Abstracts* followed closely these recommendations until the early 1970s but then began to move away from them toward the present system, which in effect subordinates P, O, N, and other atoms to C and indexes the compounds as derivatives of the organic compound having the longest carbon chain. Thus, D-glyceraldehyde 3-phosphate, formerly indexed as a derivative of D-glyceraldehyde, is now indexed as a derivative of propanal. The rationale for doing this was to facilitate the searching and indexing of the chemical literature and was never intended to replace the IUC nomenclature:




IUC Name: D-Glyceraldehyde, 3-phosphate

CAS Name: Propanal, R-(2)-hydroxy-3-phosphonooxy)-

The order of presentation for each compound in this book is as follows: (1) its IUC name; (2) its commonly used abbreviation in parentheses; (3) its molecular formula;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(4) its *Beilstein* reference if available; (5) its *Chemical Abstracts* name in italics; and (6) the year it was first reported to be a plant constituent.

## Occurrence

If the phosphorus compound is a common plant metabolite, as is often the case, its place in the metabolic sequence is illustrated by a figure. The figures in this book are composites drawn from various sources, not reproductions from a single source, except for the few instances in which a reference is cited. The shadowed boxes in the figures show metabolites inside the box and precursors and products outside the box. The box itself does not represent a cell wall or other physical barrier. If the phosphorus compound is unique for a particular plant species, which sometimes occurs owing to some metabolic quirk peculiar to that species, the original paper should be consulted for further details. A few of the plant species in which a particular phosphorus compound was first mentioned are also cited under this heading, documenting the date given under (6) above.

## Physical Properties

The physical appearance and solubility characteristics of each compound are given if the information is available. A few salts are included for each compound if useful for characterization but esters, amides, and other derivatives are not. References to spectra, chromtography and electrophoresis are selective rather than comprehensive—usually a single citation selected from those that are available.

## Synthesis

A brief survey is given of the methods that have been used to prepare each compound in the laboratory. The coverage is comprehensive with respect to the variety of methods but selective in the number of references cited, often just a single citation.

## Hydrolysis

The sensitivity of the compounds to cleavage of the phosphate group varies significantly from one compound to another. Particular attention is given to hydrolysis under acid or alkaline conditions or in the presence of heavy metal catalysts. Rate constants are given whenever possible.

## Phosphorylation

Studies under this heading are restricted to the phosphorylation of monophosphates to di-, tri-, or polyphosphates by means of known phosphorylating reagents. Some enzymatic phosphorylations appear in the metabolic pathways discussed under the section "Occurrence" and some instances of the use of phosphorylating reagents to introduce a phosphate group elsewhere in the molecule appear under the section "Synthesis."

### Structure

Studies under this heading are concerned with problems such as keto/enol tautomerism or pyranose/furanose conformation in phosphorylated sugars or preferred conformation in phytic acid.

### Extraction

No single extraction procedure is optimal for all phosphorus compounds. Attention here is focused on the methods that are most suitable for a particular compound or class of compounds. Methods that are generally applicable to a class of compounds are described in detail at the beginning of each chapter, with selected examples from the literature for methods that are widely accepted and in general use.

### Separation and Analysis

The same principles apply here. Methods that are generally applicable to the separation and analysis of the individual phosphorus compounds present in an extract are described in detail at the beginning of each chapter.

### Analysis Without Separation

Two methods in particular fall under this heading: the $^{31}$P NMR method and the enzymatic method. The first method provides a characteristic signal for each phosphorus compound, some of which are distinct enough to be useful for positive identification, and the second method may be specific enough to permit measurement of a particular phosphorus compound in a complex mixture.

### Index of Compounds

The phosphorus compounds are listed in the Index alphabetically according to their IUC names with cross-referencing to their CAS names and commonly used abbreviations.

## The Plants

### Tables

The plants are listed alphabetically in the various tables according to the binary scientific names adopted by the International Code of Botanical Nomenclature (ICBN). Their common English names are also given if known. The measurements are presented in nmol/g as the preferred format unless stated otherwise.

### Index of Plants

The plants are listed in the Index alphabetically according to their ICBN names with cross-referencing to their common names in English or other language that may be provided by the authors.

## References

In order to avoid duplication, all of the references are assembled in a single group near the end of the book.

# 1 Sugar Phosphates

This chapter covers the sugar phosphates and their derivatives with the exception of phytic acid and the inositol phosphates, which are discussed in separate chapters. The following is a complete list of the compounds treated in this chapter: Their full names are given in the introduction to each section.

| $C_n$ | Sugar phosphate | Oxidized | Reduced |
|---|---|---|---|
| $C_2$ | | GAP | |
| $C_3$ | G3P, DHAP | PEP, 2-PGA, 3-PGA, 1,3-DPGA, 2,3-DPGA | α-GP |
| $C_4$ | E4P | | |
| $C_5$ | R5P, Ru5P, Ru1,5P, Xu5P | | |
| $C_6$ | G1P, G6P, G1,6P, F1P, F6P, F1,6P, F2,6P, Gal1P, Gal6P, Man1P, Man6P | 6-PG | So1P, So6P |
| $C_7$ | Se7P, Se1,7P, Ma7P | | |
| $C_8$ | Id1,8P | | |
| $C_{12}$ | Sucrose 6′-P | | |
| $C_x$ | Starch-P | | |

For general references on this subject, see LePage and Umbreit,[3] MacDonald,[4] or Bergmeyer and Grassl[5].

## Extraction

Many plant tissues contain phosphatases that can rapidly hydrolyze the sugar phosphates during isolation. These phosphatases must be quickly and permanently destroyed.[6] The procedures most widely used in current practice employ ice-cold trichloroacetic acid (TCA) or perchloric acid (PCA), both of which kill the plant tissue and extract the sugar phosphates without degrading them. After extraction, the excess TCA is removed by extraction with ether and the excess PCA by precipitation as the water-insoluble potassium perchlorate.

> *Fully expanded leaf blades (about 0.5 g) were frozen with liquid nitrogen and ground in a mortar and pestle with 2.5 ml of 0.75*M *$HClO_4$. After 20 min, the homogenate was transferred to centrifuge tubes and the pH of the homogenate was adjusted to 5.0 with 1*M *KOH. The homogenate was centrifuged at 10,000 × g for 10 min and then the supernatant was made up to 10 ml with distilled water and immediately subjected to analysis. All the extraction procedures were carried out at 4 °C.*
>
> Murata, S.; Sekiya, J., "Effects of Sodium on Photosynthesis in *Panicum coloratum*", *Plant Cell Physiol.* **1992**, *33*(8), 1239–1242,[7] reprinted by permission of Oxford University Press, © 1992.


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Several procedures have been developed that employ different extractants. In contrast to the phospholipids or nucleotides, there is no leading reference for the extraction of sugar phosphates. Isherwood and Barrett[8] recommended the addition of 8-hydroxyquinoline to TCA as a chelating agent to prevent the loss of sugar phosphate by adsorption. Bieleski and Young[9] preferred extraction with methanol/chloroform/water (12:5:3) or methanol/chloroform/2*M* formic acid (12:5:3).[10] Others have suggested formic acid alone[11] or formic acid/ethanol.[12] Boiling 80% ethanol, once considered a useful solvent for the extraction of sugar phosphates from plant tissues,[6] is no longer recommended as it does not completely extract the soluble phosphate esters nor does it completely inactivate the phosphatases.[10,12]

## Separation and Analysis

### *(1) LePage and Umbreit Method*

This method (procedure B in Umbreit's book[3]) uses fractional precipitation with a 25% barium acetate solution of pH 8.2 and 95% ethanol to separate the TCA extract into three fractions: (1) a barium-soluble fraction containing triose-P, PEP, pentose-P, G1P, G6P, and F6P; (2) a barium-insoluble fraction containing 3-PGA and F1,6P; and (3) an ethanol-soluble fraction containing unidentified phosphorus compounds. The first two fractions are then analyzed for each component by appropriate methods.

This procedure was used to determine the levels of triose-P in potato tuber,[13] of 3-PGA in oat embryo[14] and sugar beet leaf and root,[15] of G1P, G6P, F6P, and F1,6P in potato tuber,[16] oat embryo,[14] sugar beet leaf, root and petiole,[15,17] and tomato flower ovary,[18] all carried out between 1943 and 1959. This method has been superseded by those which follow.

### *(2) Ion Exchange Chromatography (IEC) Method*

The use of IEC to separate the sugar phosphates was introduced by Benson[6] in 1950. Sugar phosphates of widely differing structure are well separated on columns containing strongly basic anion resins such as Dowex 1-X8 by stepwise or gradient elution with 0.01→0.1*N* HCl[19] or 0→8.2*M* formic acid/1.7*M* ammonium formate,[20] but the pentose, hexose, and heptose monophosphates tend to elute together because of their similar structures and dissociation constants. This problem has been solved by borate complexing. The resin can be used in the borate form, but Khym and Cohn[21] found it preferable to use the resin in the chloride form and elute the sugar phosphates stepwise with 0.025*M* $NH_4Cl$/0.0025*M* $NH_4OH$ buffer containing 0.01→0*M* borate. This procedure was used to separate the hexose monophosphates (G1P, G6P, and F6P) of kidney beans[22] and carrots.[23] The IEC method has been automated.[24]

### *(3) High-Performance Liquid Chromatography (HPLC) Method*

The behavior of the sugar phosphates toward ion exchange under HPLC conditions is similar to that of conventional IEC. Good resolution is obtained for all but the pentose and

hexose monophosphates with LiChrosorb AN (a strongly basic anion exchanger) and gradient elution with 0.005→0.4*M* $KH_2PO_4$,[25] whereas all of the sugar phosphates, including G1P, G6P, and F6P, are well separated if the mobile phase contains a 0.6 → 0*M* borate gradient.[26] The use of a solid-phase extraction (SPE) cartridge for sample cleanup is now recommended.[27]

### *(4) Paper Chromatography (PC) Method*

Two-dimensional PC has been the method of choice for the separation of plant sugar phosphates since the early 1950s. Adequate resolution is achieved with the ternary solvents used for the separation of sugars, organic acids, and the like, provided that precautions are taken to remove cations such as calcium, magnesium, or iron by the use of acid-washed paper,[6] by treatment of the plant extract with an ion exchange resin,[9] or by the addition of EDTA to the solvent.[28,29]

The ternary solvent often contains an acid for one dimension and a base, usually $NH_4OH$, for the second. The combinations of solvents listed in Table 1-1 have been found to be useful. $R_f$ values for some of the sugar phosphates of this chapter in selected pairs of ternary solvents are given in Table 1-2. Some authors prefer to report their data in the form of travel constants[9,12] or *P* values[28,31] relative to $P_i$.

The spray reagent most often used for the visualization of the sugar phosphates is that of Hanes and Isherwood, a solution of 60% perchloric acid, 4% ammonium molybdate, and 1*N* HCl in water (5:25:10:60 v:v).[34] After UV exposure to improved color development, the sugar phosphates appear as blue spots on a white background whereas inorganic phosphate has a yellow-green color.[35]

**Table 1-1** Solvent Systems for Paper Chromatography

| | Solvent Combinations | References |
|---|---|---|
| *Acidic solvents* | | |
| A1 | Methanol/formic acid/water (80:15:5) | 30 |
| A2 | *n*-Propyl acetate/formic acid/water (11:5:3) | 9 |
| A3 | *n*-Butanol/propionic acid/water (375:180:245) | 28 |
| A4 | Ethanol/*n*-BuOH/picric acid/water (32:52.5:2:15.5) | 29 |
| A5 | Ethyl acetate/acetic acid/water (3:3:1) | 31 |
| *Basic solvents* | | |
| B1 | Methanol/$NH_4OH$/water (60:10:30) | 30 |
| B2 | *n*-Propanol/$NH_4OH$/water (6:3:1) | 9 |
| B3 | 2-Methoxyethanol/2-butanone/3*N* $NH_4OH$ (7:2:3) | 31 |
| *Neutral solvents* | | |
| N1 | Methanol/1*M* ammonium acetate (7:3) | 12 |
| N2 | Ethanol/1*M* ammonium acetate (70:30) | 29 |
| N3 | Isobutyric acid/$NH_4OH$/water (57:4:39) | 12,28 |
| N4 | Phenol/water (72:28) | 6 |

**Table 1-2** Travel Constants for Some Sugar Phosphates

| Compound | PC ($R_f$)[a] | | PE[b] ($M_P$) | TLC[c] ($R_P$) | |
|---|---|---|---|---|---|
| | 1st | 2nd | | 1st | 2nd |
| $P_i$ | 0.47 | 0.74 | 100 | 100 | 100 |
| G3P | 0.45 | | 74 | | |
| DHAP | 0.43 | 0.49 | 81 | 104 | 87 |
| α-GP | | | 78 | 119 | 118 |
| 2-PGA | 0.35 | 0.69 | | | |
| 3-PGA | 0.31 | 0.69 | 107 | 80 | 88 |
| 2,3-DPGA | 0.16 | 0.69 | 132 | | |
| PEP | | | 120 | 88 | 111 |
| R5P | 0.46 | 0.41 | 70 | 109 | 62 |
| Xu5P | 0.44 | 0.34 | | | |
| Ru1,5P | 0.19 | 0.34 | | 58 | 38 |
| G1P | 0.46 | 0.26 | 64 | | |
| G6P | 0.34 | 0.23 | 64 | 77 | 61 |
| 6-PG | | | 80 | 65 | 62 |
| F6P | 0.43 | 0.34 | 62 | 81 | 66 |
| F1,6P | 0.15 | 0.34 | 100 | 57 | 32 |
| Gal1P | 0.43 | 0.23 | | | |
| Man6P | | | 64 | | |
| Se7P | 0.39 | 0.28 | 64 | | |

[a]Wawszkiewicz.[29]
[b]Wade and Morgan.[32]
[c]Feige *et al.*[33] Solvents (see Table 1-1): PC, N2 and A4; PE, 0.025*M* sodium butyrate buffer; TLC, N3 and A3.

Paper containing $^{14}C$- or $^{32}P$-labeled phosphate esters is placed in direct contact with X-ray film for 2-7 days or determined directly with the aid of a thin window gas-flow counter.[9]

### *(5) Thin-Layer Chromatography (TLC) Method*

TLC was first applied to sugar phosphates by Bieleski in 1965, but has not displaced PC despite the promise of a 20-fold increase in sensitivity in a fifth the time with no loss of resolution.[36] Two-dimensional TLC is almost always performed on TLC plates coated with 250-μ thick layers of Macherey–Nagel unbound cellulose powder, using the same ternary solvents as those used for PC. The relative positions of the phosphate esters and the patterns obtained by the two techniques are essentially the same. Travel constants relative to $P_i$ are reported in Table 1-2 for several of the sugar phosphates of this chapter; see also Cole and Ross.[12]

### *(6) Electrophoresis Methods*

The sugar phosphates can be separated from each other by paper electrophoresis (PE)[9,32] or thin layer electrophoresis (TLE),[36] but little use has been made of either method. PE was used to distinguish F1P from F6P in a potato tuber extract. The hexose monophosphates

migrate as a single band in acetate buffer[37,38] but are separated by borate buffers.[39] PE and TLE are more often used as the second dimension in two-dimensional PC/PE[38] or TLC/TLE[36,40] separations.

Buffers that have been used for this method are 0.25*M* ammonium acetate, pH 3.6 (PE, TLE),[9] 0.025*M* sodium butyrate, pH 3.2 (PE),[32] and 0.2*M* sodium borate, pH 9.5 (PE).[39] Electrophoresis is carried out at voltages of 400 V (6 h)[41] to 1000 V (16 min).[36] The paper electrophoretic mobilities ($M_P$) of some of the sugar phosphates relative to $P_i$ are given in Table 1-2; see also Bieleski and Young.[9] The mobilities on paper and thin layer plates are almost identical.[36]

## Analysis Without Separation

### *(1) $^{31}$P Nuclear Magnetic Resonance (NMR) Method*

Several plant species have been examined for the presence of sugar phosphate signals since the advent of high-field $^{31}$P FT NMR spectroscopy in the early 1980s. Roberts *et al.*[42] identified G6P in the $^{31}$P NMR spectrum of maize root tips and established that the G6P is in a cytoplasmic (pH ~7.1) rather than vacuolar (pH ~5.5) environment. The G6P signal is clearly visible in the $^{31}$P NMR spectra of maize[42,43] and sorghum[44] root tips, Jerusalem artichoke stolons,[45] and sycamore, soybean, and *Catharanthus roseus* suspension cells.[46] No other sugar phosphate has been unequivocally identified in living plant tissue by this method with the possible exception of F6P in sycamore cells.[46]

As might be expected, better resolution is attained with TCA or PCA extracts of plant tissues than with living plant tissues, and other signals can now be identified. In addition to G6P, signals for F6P,[46,47] F1,6P,[48,49] α-GP,[49–51] and 3-PGA[50,51] as well as DHAP, PEP, and 6-PG are identifiable. Quantitative data were reported for G6P and α-GP.[50]

### *(2) Enzymatic Methods*

The enzyme-coupled assay method, first modified for plant use by Rowan[52,53] in 1957, has become the method of choice for the analysis of sugar phosphates for a variety of reasons. It enables the individual sugar phosphates in a plant extract to be quantitated rapidly and accurately without prior separation and, with few exceptions, each assay is specific for the compound being analyzed. The basis of the method is the change in absorbance of NAD (or NADP) at 340 nm, which increases as NAD(P) is reduced to NAD(P)H and decreases as NAD(P)H is oxidized to NAD(P). For those reactions in which a sugar phosphate interacts directly with NAD(P) or NAD(P)H in an enzyme-catalyzed reaction, this change in absorbance provides a direct measure of the amount of sugar phosphate that causes the change. The seven reactions pertinent to the compounds of this chapter are listed in Table 1-3.

Accordingly, the substrates G3P, DHAP, α-GP, 1,3-PGA, G6P, and 6-PG are assayed directly by reaction with NAD(P) or NAD(P)H in the presence of the indicated enzyme. The other sugar phosphates listed in Table 1-3 may only be assayed after conversion to one or more of these substrates, usually by methods taken from well-known metabolic sequences; in practice, they are assayed immediately after the substrates by adding the

**Table 1-3** NAD(P) Coupled Reactions

| | Reaction | For analysis of |
|---|---|---|
| 1 | G3P + NAD → 3-PGA + NADH | G3P, E4P, R5P, Ru5P, Xu5P, F1,6P |
| 2 | DHAP + NADH → α-GP + NAD | G3P, DHAP, 3-PGA, E4P, F1P, F6P, F1,6P, F2,6P, Se1,7P |
| 3 | α-GP + NAD → DHAP + NADH | α-GP |
| 4 | 1,3-DPGA + NADH → G3P + NAD | 3-PGA, 1,3-DPGA, R5P, Ru5P, Xu5P, Ru1,5P |
| 5 | Pyruvate + NADH → Lactate + NAD | 2-PGA, 3-PGA, PEP |
| 6 | G6P + NADP → 6-PG + NADPH | E4P, G1P, G6P, G1,6P, F6P, F1,6P, Se7P |
| 7 | 6-PG + NADP → Ru5P + $CO_2$ + NADPH | R5P, 6-PG |

Enzymes: (1,4) G3P dehydrogenase [E.C. 1.2.1.12]; (2,3) α-GP dehydrogenase [E.C. 1.1.1.8]; (5) lactate dehydrogenase [E.C. 1.1.1.27]; (6) G6P dehydrogenase [E.C. 1.1.1.49]; (7) 6-PG dehydrogenase [E.C. 1.1.1.44].

appropriate enzyme (mutase, aldolase, kinase, etc.) and taking another reading at 340 nm. This process can be repeated, with the result that two or more compounds can be assayed in sequence in a single run. Further details are dealt with in later sections of this chapter since the procedures are different for each compound.

The lower limit of the spectrophotometric assay is about 10 nmol/mL. If the concentration of a metabolite is below this, the assay can be made more sensitive by fluorimetry or enzyme cycling. According to Passonneau and Lowry, these modifications reduce the lower limits of the assay to 50 and 0.01 pmol/mL, respectively.[54]

# Diose Phosphates

The parent diose (glycolaldehyde) is not a plant constituent but its oxidation product (glycolic acid) is

$$HO_2CCH_2OP(O)(OH)_2$$

Glycolic Acid Phosphate (GAP), $C_2H_5O_6P$; Beilstein **3**, $E_{III}$ 377, $E_{IV}$ 578. *Phosphonooxyacetic Acid* [1952].

## Occurrence

GAP is an important metabolite of the photorespiratory carbon oxidation cycle ($C_2$ cycle) of higher plants. It is formed in the chloroplast, together with 3-PGA, by oxidative cleavage of Ru1,5P and is subsequently hydrolyzed to glycolate by GAP phosphatase (Fig. 1-1). The participation of GAP in the $C_2$ cycle has been confirmed by numerous $^{14}C$ studies (Table 1-4), but the actual level of the metabolite in higher plants is unknown.

**FIGURE 1-1 Glycolic Acid Phosphate.** (1) Ru1,5P carboxylase-oxygenase [Rubisco, E.C. 4.1.1.39], $O_2$, $H_2O$, $Mg^{2+}$. (2) GAP phosphatase [E.C. 3.1.3.18].

**Table 1-4** Incorporation of $^{14}C$ Label into Glycolic Acid Phosphate

| No. | Plant part | Plant | | References |
|---|---|---|---|---|
| 1 | Gametophyte | *Concephalum* spp. | Liverwort | 55 |
| 1 | Young leaf | *Cucurbita* spp. | Squash | 55 |
| 1 | Young leaf | *Glycine max* (L.) Merr. | Soybean | 56 |
| 1 | Leaf | *Hordeum vulgare* L. | Barley | 57 |
| 1 | Shoot | *Isopterygium distichaceum* (Mitt.) Jaeg. | A moss | 58 |
| 1 | Young leaf | *Juniperus* spp. | Juniper | 55 |
| 1 | Young leaf | *Lycopersicon esculentum* L. | Tomato | 55 |
| 1 | Leaf | *Nicotiana tabacum* L. | Tobacco | 59 |
| 1 | Leaf | *Oryza sativa* L. | Rice | 60,61 |
| 1 | Young leaf | *Persea gratissima* Gaertn. f. | Avocado | 55 |
| 1 | Leaf | *Pisum sativum* L. | Pea | 62 |
| 1 | Prothalli | *Polystichum* spp. | A fern | 55 |
| 1 | Leaf | *Sorghum bicolor* L. | Sorghum | 63 |
| 1 | Chloroplast | *Spinacia oleracea* L. | Spinach | 20,64 |
| 1 | –, [$^{32}P$] label | | | 20 |
| 1 | Leaf | *Zea mays* L. | Maize | 57 |

The concentration of GAP in pea leaf (*Pisum sativum*) is below 2 nmol, the level of sensitivity of the enzymatic assay.[65]

## Physical Properties

Glycolic Acid Phosphate (GAP)

GAP [R.N. 13147-57-4]: Monoclinic colorless needles, mp 110-112 °C,[59] p$K_a$, 3.15, 6.40.[66] Spectra: FTIR (fig.),[67] $^{31}P$ NMR,[68] X-ray.[69] Chromatography: PC,[32] TLC,[33] IEC,[59] HPLC.[70] Electrophoresis: PE,[32] TLE.[20]

$NaC_2H_4O_6P$ [R.N. 147735-68-0]: Monoclinic crystals, d 1.98. Spectra: X-ray.[69]

$KC_2H_4O_6P$ [R.N. 147735-67-9]: Monoclinic crystals, d 2.07. Spectra: X-ray.[69]

$Ba_3(C_2H_2O_6P)_2{\cdot}4H_2O$: Crystalline solid.[71]

$BaC_2H_3O_6P{\cdot}H_2O$ [R.N. 58389-61-0]: Leaflets, sol. $H_2O$ 1.42 g/L at 20 °C,[72] insol. alcohol.[66]

$Ba_3(C_2H_2O_6P)_2{\cdot}4H_2O$: Light pearly tablets, sol. $H_2O$ 0.10 g/L at 26 °C.[73]

$(C_6H_{11}NH_3)_3C_2H_2O_5P$ [R.N. 95648-83-2]: Colorless monoclinic crystals, d 1.490. Spectra: X-ray,[74] MS.[75]

$(C_{20}H_{24}N_2O_2)_2C_2H_5O_6P{\cdot}2H_2O$ (quinine salt): White tablets, mp 148-149 °C, $[\alpha]_D^{20}$ −182.6° (50% EtOH), sparingly sol. $H_2O$, slightly sol. EtOH.[72]

$(C_{21}H_{22}N_2O_2)_2C_2H_5O_6P{\cdot}2H_2O$ (strychnine salt): White tablets, mp 221-222 °C, $[\alpha]_D^{20}$ −24.2° (50% EtOH), sparingly sol. $H_2O$, sol. EtOH.[72]

See also X-ray structure determinations on the Ca,[76] Zn,[76] cyclohexylamine,[77] and other salts.[69,76,77]

## Synthesis

GAP may be prepared (a) by phosphorylation of glycolic acid with phosphorochloridic acid[59] or of ethyl glycolate with polyphosphoric acid[78] or (b) by periodate cleavage of α-glycerophosphoric acid,[73] $F_6P$,[79] or F1,6P.[80]

## Hydrolysis

The half-life for hydrolysis of GAP to glycolic acid and $P_i$ is 90 min at 125 °C (*N* HCl)[66] or 35 min in the presence of molybdate at pH 4.0, 100 °C.[81] The rate is higher in *N* acetic acid than in *N* $H_2SO_4$.[72] The acid is much more resistant to alkaline hydrolysis: half-life ~800 h in *N* NaOH at 100 °C.[82]

## Extraction, Separation, and Analysis

GAP can be separated from 3-PGA, Ru1,5P, and other metabolites by IEC on Dowex 1 (OAc) resin,[59] by ion-pairing HPLC,[70] and other methods, but its levels in plant tissues are too low to be detected by any of these methods. Evidence for the participation of GAP in plant metabolism is based on the $^{14}CO_2$ labeling studies listed in Table 1-4. A typical experiment follows:

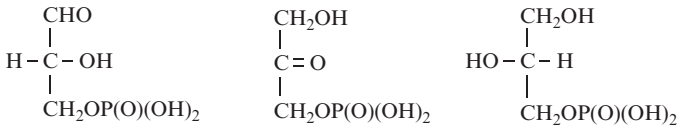
> *Barley (*Hordeum vulgare *L.) [was] grown by water culture. . .in a dark room at 25 °C for one week . . . After exposure to light (ca. 1,000 ft-c) [for periods ranging from 1 to 24 h], leaves were detached by cutting under water. . . The detached first foliage leaves were placed vertically in a fixation chamber and the bases of leaves were immersed into water . . . $^{14}CO_2$ was generated in the $CO_2$ fixation chamber by pouring 50 % (v/v) lactic acid into $NaH^{14}CO_3$ solution (65 μCi/ml) and $CO_2$ concentration was adjusted to about 0.03 %. After feeding of $^{14}CO_2$ for 3 min., the leaves were transferred to boiling ethanol (70 %, v/v) [and] extracted in sequence with boiling ethanol (50 %, v/v) and boiling water. The extracts were concentrated under reduced pressure . . . , passed through a column of Dowex 50 ($H^+$) resin [to remove amino acids, and then chromatographed on] a column of Dowex 1 ($CH_3COO^-$) resin for organic acid by Zelitch's method [59] . . . Radioactivity was measured by a liquid scintillation counter (Beckman Instruments Ltd., LS-250). After 3 hr illumination, 9.0 % of the $^{14}CO_2$ was incorporated into glycolic acid and 4.8 % into GAP.*
>
> Lee, S. H.; Ikeda, M.; Kang, Y. H.; Yamada, Y., "Studies on Carbon Fixation in Barley and Maize Leaves", *J. Fac. Agric. Kyushu Univ.* **1979**, *24*(1), 1–9,[57] reprinted by permission of the Editor-in-Chief, © 1979.

GAP was readily identified by PC in extracts of 27 plants (representing 9 phyla) that were subjected to short-term photosynthesis using $^{14}CO_2$.[55] In other experiments, a phosphate tentatively identified as [$^{32}$P]-GAP was isolated from spinach chloroplasts subjected to photosynthesis in the presence of $^{32}P_i$.[20] In all of these experiments, the $CO_2$ content of the air had to be kept low, conditions that favor photorespiration rather than

photosynthesis. If the $CO_2$ content is high, the Ru1,5P is all converted to 3-PGA (see Fig. 1-2) and no GAP is formed.

## Triose Phosphates

This group comprises two triose phosphates (G3P and DHAP), one reduced triose phosphate (α-GP), and five oxidized triose phosphates (2-PGA, 3-PGA, 1,3-DPGA, 2,3-DPGA, and PEP).




**G3P** **DHAP** **α-GP**

D-Glyceraldehyde 3-Phosphate (G3P), $C_3H_7O_6P$; Beilstein **1**, $E_{III}$ 3290, $E_{IV}$ 4117. *(R)-2-Hydroxy-3-(phosphonooxy)propanal*, R.N. 591-57-1 [1955].

Dihydroxyacetone Phosphate (DHAP), $C_3H_7O_6P$; Beilstein **1**, $E_I$ 429, $E_{III}$ 3297, $E_{IV}$ 4120. 1,3-Dihydroxy-2-propanone Phosphate; *1-Hydroxy-3-(phosphonooxy)-2-propanone*, R.N. 57-04-5 [1952].

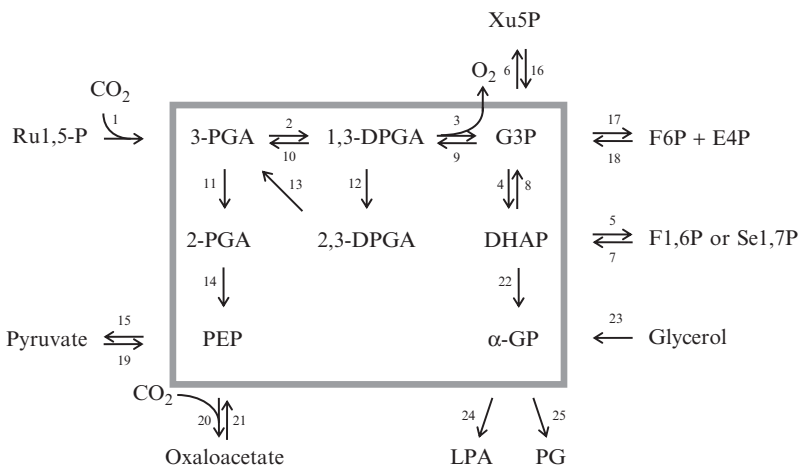
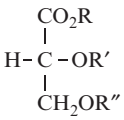
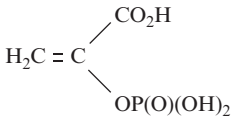



**FIGURE 1-2 Triose Phosphates.** (1) Ru1,5P carboxylase-oxygenase [Rubisco, E.C. 4.1.1.39], $CO_2$ or $O_2$, $H_2O$, $Mg^{2+}$. (2) 3-PGA kinase [E.C. 2.7.2.3], ATP, $Mg^{2+}$. (3) G3P dehydrogenase [E.C. 1.2.1.12], NADH. (4,8) Triose phosphate isomerase [E.C. 5.3.1.1]. (5,7) F1,6P aldolase [E.C. 4.1.2.13]. (6,16) Transketolase [E.C. 2.2.1.1]. (9) G3P dehydrogenase [E.C. 1.2.1.12], NAD, $Mg^{2+}$. (10) 3-PGA kinase [E.C. 2.7.2.3], ADP, $Mg^{2+}$. (11) PGA mutase [E.C. 2.7.5.3], $Mg^{2+}$. (12) DPGA mutase [E.C. 2.7.5.4]. (13) 2,3-DPGA phosphatase [E.C. 3.1.3.13]. (14) Enolase [E.C. 4.2.1.11], $Mg^{2+}$. (15,19) Pyruvate kinase [E.C. 2.7.1.40], ATP, $Mg^{2+}$, $K^+$. (17,18) Enolase [E.C. 4.2.1.11], $Mg^{+2}$. (20) PEP carboxylase [E.C. 4.1.1.31], $CO_2$, $H_2O$. (21) PEP carboxykinase [E.C. 4.1.1.49], ATP. (22) α-GP dehydrogenase [E.C. 1.1.1.8], NADH. (23) Glycerokinase [E.C. 2.7.1.30], ATP. (24) α-GP 1-O-acyltransferase [E.C. 2.3.1.15], acyl-CoA. (25) α-GP 3-phosphatidyltransferase [E.C. 2.7.8.5], CDP-DG.

α-Glycerophosphoric Acid (α-GP), $C_3H_9O_6P$. Beilstein **1**, H 517, $E_I$ 517, $E_{II}$ 275, $E_{III}$ 592, $E_{IV}$ 2333. *sn*-Glycero-3-phosphoric Acid; D-1-Glycerophosphoric Acid; *(R)-1,2,3-Propanetriol 1-(Dihydrogen Phosphate)*, R.N. 17989-41-2 [1955].




**2-PGA**, R = R″ = H, R = $P(O)(OH)_2$,
**3-PGA**, R = R′ = H, R′ = $P(O)(OH)_2$
**1,3-DPGA**, R′ = H, R = R″ = $P(O)(OH)_2$
**2,3-DPGA**, R = H, R′ = R″ = $P(O)(OH)_2$




**PEP**

D-2-Phosphoglyceric Acid (2-PGA), $C_3H_7O_7P$; Beilstein **3**, $E_{II}$ 262, $E_{III}$ 846, $E_{IV}$ 1050. Glyceric Acid 2-(Dihydrogen Phosphate); *(R)-3-Hydroxy-2-(phosphonooxy)propanoic Acid*, R.N. 3443-57-0; see also 2553-59-5 [1934].

D-3-Phosphoglyceric Acid (3-PGA), $C_3H_7O_7P$; Beilstein **3**, $E_{II}$ 262, $E_{III}$ 847, $E_{IV}$ 1051. Glyceric Acid 3-(Dihydrogen Phosphate); Nilsson ester; *(R)-2-Hydroxy-3-(phosphonooxy) propanoic Acid*, R.N. 3443-58-1; see also 820-11-1 [1930].

D-1,3-Diphosphoglyceric Acid (1,3-DPGA), $C_3H_8O_{10}P_2$; Beilstein **3**, $E_{III}$ 851. Negelein ester; *(R)-1,3-Bis(phosphonooxy)propanoic Acid,* R.N. 38163-82-0; see also 1981-49-3 [1988].

D-2,3-Diphosphoglyceric Acid (2,3-DPGA), $C_3H_8O_{10}P_2$; Beilstein **3**, $E_{II}$ 262, $E_{III}$ 850, $E_{IV}$ 1052. Greenwald ester; *(R)-2,3-Bis(phosphonooxy)propanoic Acid*, R.N. 14438-19-8; see also 138-81-8 [1925].

Phosphoenolpyruvic Acid (PEP), $C_3H_5O_6P$; Beilstein **3**, $E_{III}$ 682, $E_{IV}$ 977. 2-Hydroxyacrylic Acid Dihydrogen Phosphate; *2-Phosphonooxy-2-propenoic Acid*, R.N. 138-08-9 [1934].

## Occurrence

G3P, DHAP, 3-PGA, and 1,3-DPGA are metabolites of the photosynthetic carbon reduction cycle (Calvin cycle) of higher plants (Fig. 1-2, reading clockwise). In step 1, Ru1,5P combines with $CO_2$ and water to form an intermediate which is immediately cleaved to two molecules of 3-PGA. In step 2, 3-PGA is phosphorylated by ATP to 1,3-DPGA. In step 3, 1,3-DPGA is reduced by NADH to G3P with the loss of the phosphate group at $C_1$. In step 4, G3P is converted into its isomer DHAP. In step 5, DHAP condenses with G3P forming F1,6P or with E4P forming Se1,7P. In step 6, G3P reacts with F6P forming Xu5P and E4P or with Se7P forming Xu5P and R5P. These reactions all occur within the chloroplast, found only in the green leaf.

G3P, DHAP, 3-PGA, and 1,3-DPGA are also metabolites of the Embden-Meyerhof-Parnas glycolysis pathway (Fig. 1-2, reading counterclockwise), in which F1,6P is degraded to 3-PGA (steps 7-10). In step 11, 3-PGA is converted to its isomer 2-PGA; 2,3-DPGA, a

cofactor for the enzyme involved in this conversion, is formed from 1,3-DPGA and degraded to 3-PGA as shown in steps 12 and 13.[5] In step 14, 2-PGA is dehydrated to PEP and in step 15 the PEP is hydrolyzed to pyruvate. These reactions all take place in the cytoplasm outside any organelle.

G3P is also involved in the pentose phosphate respiratory pathway. It is formed from Xu5P by the transfer of the terminal two-carbon segment to either E4P or R5P (step 16) and reacts with Se7P to form E4P and F6P (step 17). These reactions take place in the cytoplasm, and in the chloroplast in periods of darkness. The metabolite levels are highest when the respiration rate is high, which occurs in the young plant before flowering and in the young leaves and roots of the mature plant.

PEP is a metabolite of $C_4$ plants, which differ from the usual $C_3$ plants in that the initial product of $CO_2$ fixation is malate or aspartate rather than 3-PGA. In step 19, pyruvate is phosphorylated to PEP by ATP. In step 20, PEP combines with $CO_2$ and $H_2O$ to form oxaloacetate and $P_i$. Step 19 occurs within the chloroplast whereas step 20 occurs outside, in the mesophyll of the green leaf. In one $C_4$ subgroup, PEP is formed from oxaloacetate and ATP in a reaction catalyzed by PEP carboxykinase (step 21). This enzyme is located in most cases in the cytoplasm of green leaf tissue.

α-GP is a precursor of lysophosphatidic acid (LPA, step 24) and of the terminal glycerol unit of phosphatidylglycerol (PG, step 25). It is formed from DHAP by reduction with NADH (step 22) or from glycerol by phosphorylation with ATP (step 23).

## Physical Properties

D-Glyceraldehyde 3-Phosphate

G3P [R.N. 591-57-1]: $[\alpha]_D^{25}$ +14.5° (0.1*N* HCl)[83] $\Delta G^\circ$ −105.9 kcal/mol.[84] Spectra: $^{13}C$ NMR.[85] Chromatography: PC,[9,32] TLC,[12] IEC,[86,87] HPLC.[26] Electrophoresis: PE,[32] zone,[88] CZE,[89] CE,[90] isotachophoresis.[88]

$CaC_3H_5O_6P{\cdot}2H_2O$: White crystals.[91]

More extensive data are available on synthetic G3P, which also contains the L-isomer: D,L-G3P [R.N. 142-10-9]: Very hygroscopic granular powder, begins to melt to a glass above 75 °C[92]; readily soluble in water; p$K_a$ 2.10, 6.75.[93] Spectra: UV, IR (fig.),[94] FTIR (fig.),[95] GC-MS,[96] $^1H$ and $^{13}C$ NMR,[97] $^{31}P$ NMR (fig.).[98] Chromatography: HPLC,[99] HPLC-MS-MS.[100]

Dihydroxyacetone Phosphate

DHAP [R.N. 57-04-5]: p$K_a$ 1.77, 6.45[93]; unstable at pH > 6[101]; $\Delta G^\circ$ −106.1 kcal/mol.[84] Spectra: UV,[102] IR (fig.),[103] FTIR (fig.),[95] GC-MS,[96] $^1H$ NMR (fig.),[103] $^{13}C$ NMR (fig.),[85] $^{31}P$ NMR (fig.).[104] Chromatography: PC,[32] TLC,[105] IEC,[86] HPLC,[106] HPLC-MS-MS,[100] IC.[107] Electrophoresis: PE,[32] TLE,[105] zone,[88] CZE,[89] CE,[90] isotachophoresis.[88]

$KC_3H_6O_6P$: Solid, sol. $H_2O$, insol. EtOH.[101]

$CaC_3H_5O_6P{\cdot}1/2H_2O$: Amorphous solid, often with irregular leaflets; unstable even at 0 °C.[108]

$BaC_3H_5O_6P{\cdot}1/2H_2O$: Like the calcium salt.[108]

α-Glycerophosphoric Acid

α-GP [R.N. 17989-41-2]: Thick, colorless syrup, readily sol. $H_2O$, methanol and ethanol, insol. ether; $[\alpha]_D$ −1.45° (2*N* HCl).[109] Spectra: FTIR (fig.),[110] GC-MS,[96] $^{31}$P NMR.[68] Chromatography: TLC.[111]

$Na_2C_3H_7O_6P$: $[\alpha]_D$ 0 ($H_2O$).[112]

$BaC_3H_7O_6P$: Crystals, $[\alpha]_D$ 0° ($H_2O$)[109]; solubility in water, 2.1% at 18 °C,[112] less soluble in hot water.[109]

$Ag_2C_3H_7O_6P$: Colorless needles, $[\alpha]_D^{20}$ +0.8° ($H_2O$).[113]

$(C_{20}H_{24}N_2O_2)_2C_3H_9O_6P$ (quinine salt): White needles, mp 155 °C, $[\alpha]_D$ −150.3° (ethanol)[112]; sol. ethanol, hot water, insol. cold water.[114]

$C_{21}H_{22}N_2O_2{\cdot}C_3H_9O_6P$ (strychnine salt): Prisms, mp 22 °C, $[\alpha]_D$ −21.99° ($H_2O$).[112]

More extensive data is available on synthetic α-GP, which also contains the L-isomer:

DL-α-GP [R.N. 57-03-4]: p$K_1$ 1.40,[93] p$K_2$ 6.648, $\Delta G^\circ$ 9081 cal, $\Delta H^\circ$ −749 cal, $\Delta S^\circ$ −33.0 cal/deg at 25 °C[115]; $\Delta G^\circ$ −114.2 kcal/mol[84]; LCAO-MO.[116] Spectra: Far-UV,[117] $^1$H NMR,[118] $^{13}$C NMR (fig.).[118] Chromatography: PC,[9] TLC,[119] IEC,[120] HPLC,[121] cellulose column,[122] IC,[107] GC (fig.).[123] Electrophoresis: PE.[9]

DL-$Na_2C_3H_7O_6P{\cdot}6H_2O$ [R.N. 34363-28-5]: Nonhygroscopic, very hard twinned crystals[124] or monoclinic truncated trapezoids, d 1.606[125]; heat of combustion $Q_M$ 1645 kJ/mol.[126] Spectra: X-ray.[125]

DL-$CaC_3H_7O_6P{\cdot}2H_2O$ [R.N. 55128-84-2]: X-ray (fig.).[127] Anhydrous salt: Square leaflets, solubility in water 1.9% at 13 °C.[128]

D-2-Phosphoglyceric Acid

2-PGA [R.N. 3443-57-0; see also 2553-59-5]: $[\alpha]_D^{21}$ +13.0° (1*N* HCl),[129] p$K_a$ 3.62, 6.97,[130] and 1.8[129]; conformation[131,132]; $\Delta G^\circ$ −158.0 kcal/mol.[84] Spectra: GC-MS,[96] $^1$H NMR,[131] $^{13}$C NMR,[132] $^{31}$P NMR.[68] Chromatography: PC,[9] TLC,[133] IEC,[134] HPLC,[135] IC.[107] Electrophoresis: PE,[9] TLE,[36] zone,[88] CZE,[136] CE.[90]

$Na_3C_3H_4O_7P{\cdot}5H_2O$: long needles, $[\alpha]_D^{22}$ +3.6° ($H_2O$), sol. $H_2O$, insol. MeOH, ether.[129]

Hexahydrate [R.N. 99470-03-8]: Orthorhombic plates, d 1.76; X-ray.[137]

$Ag_3C_3H_4O_7P$: White cryst.[138]

$BaC_3H_5O_7P{\cdot}1.5H_2O$: Leaflets.[139]

D-3-Phosphoglyceric Acid

3-PGA [R.N. 3443-58-1; see also 820-11-1]: $[\alpha]_D^{20}$ −13.8°,[140] p$K_a$ 3.59, 6.76,[130] and 1.42[93]; countercurrent distribution[141]; conformation[132]; $\Delta G^\circ$ −160.1 kcal/mol,[104] −3.1 kcal/mol.[142] Spectra: FTIR (fig.),[67] GC-MS,[96] $^1$H NMR (fig.),[132] $^{13}$C NMR,[132] $^{31}$P NMR.[68] Chromatography: PC,[9,32] TLC,[133] GC,[143] IEC,[134] HPLC,[70,144] IC (fig.).[107] Electrophoresis: PE,[32] TLE,[36] zone,[88] isotachophoresis,[88] CZE,[136] CE.[89]

$Na_3C_3H_4O_7P$ [R.N. 61546-67-6]: $[\alpha]_D$ +11.39° ($H_2O$).[145]

$Na_2C_3H_5O_7P$ [R.N. 80731-10-8]: Monoclinic cryst., d 2.143,[146] $[\alpha]_D$ +7.71° ($H_2O$)[145]; X-ray.[146]
$KC_3H_6O_7P$ [R.N. 164034-33-7]: Colorless orthorhombic prisms, d. 1.85. Spectra: X-ray.[147]
$BaC_3H_5O_7P•2H_2O$ [R.N. 86879-11-0]: Monoclinic plates, d 2.53,[148] $[\alpha]_D$ +5.10° ($H_2O$).[145] Spectra: X-ray,[148] XPS.[149]
$CdC_3H_5O_7P•3H_2O$ [R.N. 32690-78-1]: Monoclinic prisms, d 2.203; X-ray.[150]
See also X-ray structure determinations on the calcium and cyclohexylamine salts.[147,151,152]

1,3-Diphosphoglyceric Acid

1,3-DPGA [R.N. 38163-82-0; see also 1981-49-3]: Unstable, decomposing spontaneously into 3-PGA and phosphoric acid; $\Delta G^{\circ}$ −160.0 kcal/mol.[84] Spectra: UV,[153] $^{31}$P NMR.[154] Chromatography: HPLC.[99]
$(C_{21}H_{22}N_2O_2)_4C_3H_8O_{10}P_2$ (strychnine salt): Crystals, unstable in the dry state, insol. $H_2O$.[153]

D-2,3-Diphosphoglyceric Acid

2,3-DPGA [R.N. 14438-19-8; see also 138-81-8]: Hygroscopic sirup, readily sol. alcohol, $[\alpha]_D^{20}$ −2.29°,[155] p$K_a$ 6.39, 7.39 (apparent), 6.99, 7.28 (intrinsic)[156]; conformation[157]; enthalpy of ionization 0.0 ± 0.3 kcal/mol[158]; $\Delta G^{\circ}$ −158.2 kcal/mol,[84] −11.3 kcal/mol.[142] Spectra: FTIR (fig.),[67] GC-MS,[96] $^1$H NMR (fig.),[159] $^{31}$P NMR.[68] Chromatography: PC,[32] TLC,[160] IEC,[86] HPLC.[135,161] Electrophoresis: PE,[32] zone,[88] isotachophoresis.[88]
$Na_5C_3H_3O_{10}P_2$: $[\alpha]_D$ −3.5° ($H_2O$).[162]
Ca salt: Amorph., insol. $H_2O$.[155]
Ba salt: Amorph., insol. $H_2O$[155] Spectra: IR.[159]

Phosphoenolpyruvic Acid

PEP [R.N. 138-08-9]: Slightly hygroscopic triclinic plates, mp 103 °C, d 1.72,[163] p$K_a$ 1.41, 3.56, 6.22[164]; $\Delta G^{\circ}$ −15.2 kcal/mol, $\Delta H^{\circ}$ −14.3 kcal/mol, $\Delta S^{\circ}$ +3 cal/deg/mol[165]; MO,[166] LCAO-MO,[116] $\Delta E$ (*ab initio* calcn.).[167] Spectra: UV (fig.),[168] GC-MS,[96] $^1$H NMR,[169] X-ray.[163] Chromatography: PC,[9,32] TLC,[36] IEC,[86] HPLC,[135] IC.[107] Electrophoresis: PE,[32] TLE,[36] zone,[88] CZE,[89] isotachophoresis.[88] It is best handled and stored in the form of its stable, crystalline monopotassium salt.[170]
$NaC_3H_4O_6P•H_2O$ [R.N. 77617-15-3]: Monoclinic prisms, d 1.89[171]; Spectra: IR,[172] X-ray.[171]
$AgBaC_3H_2O_6P•2H_2O$ [R.N. 129176-93-8]: Colorless prisms (photo.).[173]
$(C_6H_{11}NH_2)C_3H_5O_6P$ [R.N. 10526-80-4]: Orthorhombic needles, d 1.36 or oblique monoclinic parallelepipeds, d 1.36 (two polymorphic forms). Spectra: X-ray.[174]
$(C_6H_{11}NH_2)_3C_3H_5O_6P$ [R.N. 35556-70-8]: Cryst., dec. 155-180 °C.[168] Monohydrate: Colorless orthorhombic crystals, d 1.22. Spectra: X-ray.[175]

See also X-ray structure determinations on the K,[176] Ca,[177] ammonium,[178] and other[179,180] salts.

## Synthesis

G3P may be prepared (a) by phosphorylation of 2-*O*-benzyl D-glyceraldehyde dimethyl acetal with diphenyl phosphorochloridate[83] or of (*R*)-glycidaldehyde diethyl acetal with $Na_2HPO_4$,[181] (b) by cleavage of R5P, F6P, or F1,6P with lead tetraacetate[85,91] or periodate,[71] or (c) by enzymatic cleavage of F1,6P with zymohexase in the presence of hydrazine.[182]

DHAP may be prepared (a) by phosphorylation of 1,3-dihydroxyacetone with $POCl_3$[108] or ethyl metaphosphate,[183] (b) by phosphorylation of *O*-acetyl-1,3-dihydroxyacetone[103,184] or 2,5-diethoxy-*p*-dioxane-2,5-dimethanol[185,186] with diphenyl phosphorochloridate or cyanoethyl phosphate, (c) by hydrolysis of bromoacetone phosphate,[187] (d) by enzymatic phosphorylation of 1,3-dihydroxyacetone with glycerokinase and ATP in the presence of PEP or acetyl phosphate,[101] (e) by enzymatic cleavage of F1,6P with zymohexase in the presence of sodium bisulfite,[188] or (f) by enzymatic oxidation of α-GP with α-GP oxidase in the presence of catalase.[189] Because of its instability, DHAP is best stored as a ketal from which it can be prepared when needed.

α-GP may be prepared (a) by phosphorylation of *O*,*O*-isopropylidene-D(+)-glycerol with phosphorus oxychloride, (b) by fermentation of glucose in the presence of $P_i$ and fluoride,[113] (c) by resolution of synthetic DL-α-GP,[112] or (d) by phosphorylation of glycerol with glycerol kinase, preferably immobilized on polyacrylamide gel, in the presence of acetyl fluoride and ATP.[190] Hydrolysis of lecithin with either acid or alkaline catalysts is unsuitable because of migration of the phosphate group, resulting in a product contaminated with β-GP and D-α-GP.[191]

2-PGA may be prepared (a) by phosphorylation of methyl 3-*O*-benzyl D-glycerate with diphenyl phosphorochloridate,[129] (b) by acid-catalyzed isomerization of 3-PGA,[192] (c) by periodate cleavage of D-gluconic acid 2-phosphate,[193] or by selective degradation of the L-isomer of DL-2-PGA with *Leuconostoc mesenteroides*.[194]

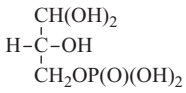
3-PGA may be prepared (a) by phosphorylation of D-(−)-glyceric acid with ethyl metaphosphate,[138] (b) by the action of baker's yeast on sugar phosphate (sucrose and $NaH_2PO_4$) in the presence of acetaldehyde and NaF,[140] or (c) by selective degradation of the L-isomer of DL-3-PGA with *L. mesenteroides*.[194]

1,3-DPGA may be prepared by enzymatic phosphorylation of G3P with phosphoric acid in the presence of acetaldehyde[153] or sodium pyruvate.[195] 2,3-DPGA may be prepared by phosphorylation of methyl D-glycerate with diphenyl phosphorochloridate.[162]

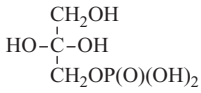
PEP may be prepared (a) by phosphorylation of pyruvic acid[173] or 3-chlorolactic acid[196] with $POCl_3$ or of methyl pyruvate with polyphosphoric acid,[78] (b) by the reaction of bromopyruvic acid with trimethyl phosphite,[197] tribenzyl phosphite,[172] or dimethyl trimethylsilyl phosphite,[198] or (c) by enzymatic rearrangement of 2-PGA with enolase.[129]

## Structure

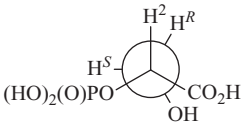
G3P exists in aqueous solution as a 29:1 mixture of the *gem*-diol **1** and free aldehyde, but only the latter is active as a substrate for G3P dehydrogenase [E.C. 1.2.1.12]. The first-order rate constant $k$ for the conversion of diol to aldehyde is 0.087 $s^{-1}$ at 20 °C.[199] In aqueous solutions of DHAP, however, the ratio of keto to *gem*-diol **2** is 3:2.[103,104] About 1.0% of the DHAP is in the enol form at pH 7 and 20 °C[200]. The preferred conformation of 2-PGA in aqueous solution is the *gauche* form **3** in which the alcoholic OH is hydrogen-bonded to the carboxyl group.[131]



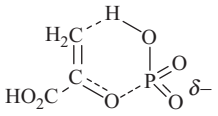

**1** (G3P)




**2** (DHAP)




**3** (2-PGA)




**4** (PEP)

## Hydrolysis

G3P is completely hydrolyzed by 1*N* acid to methylglyoxal and $P_i$ in 60 min at 100 °C. [83] The rate constant $k$ is $6.25 \times 10^{-4}$ $s^{-1}$ in 1*N* HCl at 100 °C.[108] Exposure to 2*N* NaOH for 20 min completely hydrolyzes G3P to $P_i$ and lactic acid.[201] In alkaline media, methylglyoxal is rapidly converted to lactic acid. For the kinetics of hydrolysis of DL-G3P in the neutral region (pH 5-9), see Kozlova *et al.*[202]

DHAP, which is isomeric with G3P, exhibits similar behavior. The rate constant $k$ is $5.62 \times 10^{-4}$ $s^{-1}$ for hydrolysis in 1*N* HCl at 100 °C.[108] Exposure to 2*N* NaOH at room temperature hydrolyzes DHAP completely to $P_i$ and lactic acid.[201] The rate increases with KOH concentration up to 0.5 mol/L and remains the same at higher concentrations.[203]

The hydrolysis of DL-α-GP is catalyzed by molybdate,[204] Pb(II),[205] Ce(III),[206] La(III),[206] and Th(IV),[207] but not by Zr(IV).[208] In the pH 3-7 range, where the monoanion $HA^-$ is predominant, the rate constant for the hydrolysis of DL-α-GP to glycerol at 100 °C is $1.35 \times 10^{-5}$ $s^{-1}$ compared to $2.77 \times 10^{-5}$ $s^{-1}$ for β-GP. In solutions of pH < 3, however, the rates become equal owing to acid-catalyzed rearrangement.[209] At lower pH values the rates fall to a minimum (neutral acid $H_2A$), then increase linearly with acid concentration.[210] Experiments with $^{18}O$-enriched water show that only P—O bond fission occurs despite differences in mechanism between $HA^-$ and $H_2A$.[210]

Both isomers are stable to boiling 0.025*N* NaOH.[211] α-GP is readily hydrolyzed by acid phosphatase, which is highly specific for this substrate,[212] but less rapidly than β-GP by alkaline phosphatase.[213]

2-PGA is hydrolyzed to D-glyceric acid when heated in 1*N* HCl in a sealed tube for 18 h at 125 °C, but under milder conditions (0.25*N* HCl, 75 °C) it rearranges to 3-PGA without releasing any inorganic phosphate.[129] Owing to this rearrangement, the rates of acid hydrolysis of 2-PGA and 3-PGA are identical.[66] The rate constant $k$ is $2.58 \times 10^{-5}$ $s^{-1}$.[139]

For the effect of pH over the 2-10 range on the hydrolysis of 2-PGA at 100 °C, see Wold and Ballou.[214] At pH 4 and 100 °C, in the presence of molybdate catalyst, half of the phosphate in 2-PGA was released in 35 min whereas 3-PGA was unaffected.[81] 3-PGA is unusually resistant to acids and alkalis, and also to thermal degradation.[140] Hydrolysis of 3-PGA in the neutral region is catalyzed by Th(IV),[215] Ce(III),[216] La(III),[216] and UV radiation.[217]

1,3-DPGA decomposes spontaneously in aqueous solution. The rate constant is 0.026 $min^{-1}$ at 38 °C and pH 7.2 and is catalyzed by acids and bases.[153] Experiments with $^{18}O$-labeled water show that 1,3-DPGA is an acyl donor toward GDH in the dehydrogenase reaction (Fig. 1-2, step 3) and a phosphate donor toward ADP in the 3-PGA kinase reaction (Fig. 1-2, step 10). The bond cleavage is C—O in the former and P—O in the latter.[218]

2,3-DPGA is extraordinarily resistant to acid hydrolysis; it requires boiling for days with 5% $H_2SO_4$ to effect complete decomposition to D(−)-glyceric acid.[219] In 1*N* HCl at 125 °C the hydrolysis proceeds stepwise, the initial rate being $5.97 \times 10^{-5}$ $s^{-1}$ and the final rate $2.80 \times 10^{-5}$ $s^{-1}$. If hydrolysis is interrupted after 2 h, the product is found to be a mixture of 2-PGA and 3-PGA.[139]

Hydrolysis of PEP yields only $P_i$ and pyruvic acid over the pH 0-8 range at 75 °C. The rate constants for the dianion $HA^{2-}$, monoanion $H_2A^-$, and neutral acid $H_3A$ are all abnormally high, in keeping with the high-energy character of PEP in relation to other monoalkyl phosphates. A mechanism was proposed in which the expulsion of metaphosphate is enhanced by the formation of cyclic transition state, **4**.[164] Hydrolysis of PEP at 75 °C is catalyzed by $>10^6$-fold by Hg(II) via addition to the enol double bond, and 10-fold by Cu(II) via a chelation or complexation mechanism. Other metal ions are ineffective.[220]

## Metal Ion Complexes

DL-α-GP forms binary 1:1 complexes with metal(II) ions. The extent of complexing can be determined by potentiometric titration. Stability constants have been reported for the Mg(II) and Ca(II) complexes.[221]

## Separation and Analysis

### *(1) LePage and Umbreit Method*[3]

G3P and DHAP appear in the barium-soluble fraction of the TCA extract (see Chapter 8, pp. 459-460). They are determined together as triose phosphate (TP) by the amount of $P_i$ released in 20 min at room temperature with 2*N* NaOH. 3-PGA appears in the barium-insoluble fraction of the TCA extract and is analyzed by a colorimetric method. The LePage and Umbreit method has been superseded by those which follow.

### *(2) Chromatographic Methods*

The triose phosphates can be separated from other phosphate esters by IEC or HPLC after extraction with perchloric acid or trichloroacetic acid, but their separation from each other requires two-dimensional PC/PC, PC/PE, TLC/TLC, or TLC/TLE. Basic solvents like

*n*-propanol/$NH_4OH$/$H_2O$[9,29] should be avoided in the case of G3P or DHAP because of their extreme sensitivity to base, but neutral solvents that contain ammonium salts such as ammonium acetate or ammonium isobutyrate are acceptable.[12,28] 2-PGA and 3-PGA should be separable from each other by these methods but there are no examples of this in Table 1-5. α-GP can be separated from other phosphate esters by GLC after extraction with perchloric acid.[255] Quantitative data have been reported for TP, 2-PGA, and 3-PGA by the IEC method, for α-GP by the GLC method, and for DHAP, 3-PGA, and PEP by the PC/PC and PC/PE methods.

PEP is best extracted from plant tissues as the 2,4-dinitrophenylhydrazone and separated from other α-keto acid DNPs by two-dimensional PC:

> *5 g fresh weight of each plant part [was] homogenised with 0.25 ml cold sulphuric acid, 50 mg of 2,4-dinitrophenylhydrazine (2,4-DNPH) and 60 ml of 80 % ethanol. . . , kept at room temperature with occasional stirring for an hour . . ., [and] centrifuged. The residue [was extracted four times with] 20 ml of cold ethyl acetate . . . Extracts were mixed . . . evaporated to dryness . . . [and] extracted thrice with 2 ml 10 % $Na_2CO_3$. The solution of keto acid hydrazones (Na salts) was diluted to a final volume of 10-15 ml with water. The combined extracts were then reextracted twice with 2 ml aliquots of ethyl acetate [to remove] the uncombined hydrazones . . . The carbonate solution was cooled and adjusted to pH 2.0 with ice-cold conc. $H_2SO_4$ and extracted thrice with ethyl acetate. The combined extracts were evaporated to dryness under a current of cold air. Small crystals of keto acid hydrazones [were] found in the residue . . . Different DNP's were separated by two-dimensional paper chromatography using n-butanol:ammonia:water (16:3:1) and n-butanol:ethanol: water (5:1:4) for the 1st and 2nd direction, respectively. Keto acids were detected on the chromategrams by their yellow spots and identified by their $R_f$ values . . . For quantitative analysis, keto acid spots . . . were eluted with 5 ml of 0.2*M *$Na_2CO_3$ and [read] in a photoelectric colorimeter at 420 nm.*
>
> Mukherjee, D., "Keto Acids and Amino Acids Changes in Leaves, Flowers and Fruits of *Cajanus cajan*", *J. Ind. Bot. Soc.* **1974**, *53*(1/2), 115–118,[241] reprinted by permission of the Chief Editor, © 1974.

## Analysis Without Separation

### *(1) $^{31}P$ NMR Method*

DHAP, α-GP, 3-PGA, and PEP have been identified in perchloric acid extracts of beans, spinach, and sycamore by high-field FT $^{31}P$ NMR spectroscopy.[49–51] A signal assigned to 3-PGA appears in the spectrum of compressed spinach leaf.[50]

### *(2) Enzymatic Method*

In this method, G3P and DHAP are analyzed by reactions coupled to the oxidation of NADH to NAD (Table 1-3, reaction 2). In the following procedure, they are analyzed

**Table 1-5** Triose Phosphates in Plants*

| No. | Plant part | Method | G3P | DHAP | TP | α-GP | 2-PGA | 3-PGA | DPGA | PEP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acer pseudoplatanus* L. (Sycamore Maple) | | | | | | | | | | | |
| 1 | Cell suspension | $^{31}$P NMR | | | | + | | + | | | 51 |
| *Actinidia deliciosa* Liang and Ferg. (Kiwi) | | | | | | | | | | | |
| 3 | Fruit | Enzym. | | | | | | | | 5.1 | 222 |
| *Albizia lebbeck* (L.) Benth. (Lebbek Tree) | | | | | | | | | | | |
| 1 | Leaf[a] | PC/PC | | | | | | | | 720 | 223 |
| 1 | Flowering bud[a] | PC/PC | | | | | | | | 640 | 223 |
| 1 | Flower[a] | PC/PC | | | | | | | | 720 | 223 |
| *Amaranthus caudatus* L. (Love-Lies-Bleeding) | | | | | | | | | | | |
| 1 | Leaf[b] | Enzym. | | | 714 | | | 667 | | 147 | 224 |
| *Amaranthus cruentus* L. (Purple Amaranth) | | | | | | | | | | | |
| 1 | Leaf[c,d] | Enzym. | | | | | | 78 | | | 225 |
| *Amaryllis vittata* L'Her. (Amaryllis) | | | | | | | | | | | |
| 1 | Pollen[d] | Enzym. | 440 | 130 | | | | | | 1170 | 226 |
| *Apium graveolens* L. var. *dulce* (Celery) | | | | | | | | | | | |
| 1 | Petiole vascular bundle | PC/PC | | | | | | + | | | 227 |
| *Arachis hypogaea* L. (Groundnut) | | | | | | | | | | | |
| 1 | Leaf[a] | PC/PC | | | | | | | | 30 | 228 |
| *Arbutus unedo* L. (Strawberry Tree) | | | | | | | | | | | |
| 1 | Leaf[b,d] | Enzym. | | | 25 | | | 391 | | | 229 |
| *Arum maculatum* L. (Cuckoopint) | | | | | | | | | | | |
| 1 | Club | Enzym. | | | | | 13.2 | 156.8 | | 23.2 | 230 |
| 1 | –, cytosol and vacuole[b] | Enzym. | | | 130 | | | 11 | | | 231 |
| *Avena sativa* L. (Oats) | | | | | | | | | | | |
| 1 | Seed | Enzym. | | | | | | 0 | | 0 | 232 |
| 1 | 1-day seed embryo[f] | LePage | | | | | | 102 | | | 14 |
| 1 | Leaf mesophyll protoplast, chloroplast[b] | Enzym. | | | 42 | | | 43 | | | 231 |
| 1 | –, mitochondria[b] | Enzym. | | | 28 | | | 61 | | | 231 |
| 1 | –, androecium[a] | PC/PC | | | | | | | | 1040 | 233 |
| 1 | –, gynoecium[a] | PC/PC | | | | | | | | 1760 | 233 |
| 1 | Immature fruit[a] | PC/PC | | | | | | | | 1200 | 233 |
| 1 | Mature fruit[a] | PC/PC | | | | | | | | 0 | 233 |
| 1 | Root[a] | PC/PC | | | | | | | | 800 | 234 |
| 1 | Seed, hypocotyl[a] | PC/PC | | | | | | | | 5600 | 234 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, cotyledon[a] | PC/PC | | | | | | | 912 | 234 |
| *Bauhinia purpurea* L. (Purple Bauhinia) | | | | | | | | | | |
| 1 | Leaf[a] | PC/PC | | | | | | | 800 | 233 |
| 1 | Flower, calyx[a] | PC/PC | | | | | | | 1440 | 233 |
| 1 | –, corolla[a] | PC/PC | | | | | | | 1600 | 233 |
| *Bauhinia variegata* L. (Orchid Tree) | | | | | | | | | | |
| 1 | Flowering bud[a] | PC/PC | | | | | | | 1140 | 235 |
| 1 | Leaf [a] | PC/PC | | | | | | | 720 | 233 |
| 1 | Flower, corolla[a] | PC/PC | | | | | | | 1140 | 233 |
| 1 | –, androecium[a] | PC/PC | | | | | | | 2720 | 233 |
| 1 | –, other parts[a] | PC/PC | | | | | | | 0 | 233 |
| 1 | Immature seed[a] | PC/PC | | | | | | | 400 | 233 |
| *Beta vulgaris* (L.) Banks (Sugar Beet) | | | | | | | | | | |
| 1 | Root, stored | LePage | | | | | 240 | | | 15 |
| 1 | –, vegetating | LePage | | | | | 260 | | | 15 |
| 1 | Leaf | LePage | | | | | 1040 | | | 15 |
| 1 | Leaf[b,d] | Enzym. | | | 51 | | 432 | | | 236 |
| *Beta vulgaris* L. ssp. *rapacea* (Koch) (Döll Forage Beet) | | | | | | | | | | |
| 1 | Leaf[g] | Enzym. | | | | | 2110 | | | 237 |
| *Brassica campestris* L. (Turnip Rape) | | | | | | | | | | |
| 1 | Pod, deseeded | Enzym. | 14.3 | 17.3 | | | 830 | | | 238 |
| *Brassica napus* L. (Rape) | | | | | | | | | | |
| 1 | Leaf[e] | Enzym. | | 9.5 | | | 81.9 | | | 239 |
| *Brassica pekinensis* (Lour.) Rupr. (Pe-tsai) | | | | | | | | | | |
| 1 | Petiole vascular bundle | PC/PC | | | | | + | | | 36 |
| 1 | Petiole vascular bundle | TLC/TLC | | | | | + | | + | 36 |
| 1 | Petiole vascular bundle | TLC/TLE | | | | | + | | + | 36 |
| *Brassica rapa* L. (Turnip Rape) | | | | | | | | | | |
| 1 | Vascular bundle | TLC/TLC | | | | | + | | | 240 |
| *Cajanus cajan* (L.) Mill. (Pigeon Pea) | | | | | | | | | | |
| 1 | Leaf[a] | PC/PC | | | | | | | 1920 | 241 |
| 1 | Open flower[a] | PC/PC | | | | | | | 1440 | 241 |
| 1 | Young flower[a] | PC/PC | | | | | | | 1300 | 241 |
| *Capsicum annuum* L. (Bell Pepper) | | | | | | | | | | |
| 1 | Leaf | Enzym. | 266 | 178 | | 88 | 86 | | 341 | 242 |
| *Catharanthus roseus* (L.) G. Don (Madagascar Periwinkle) | | | | | | | | | | |
| 1 | Suspension cells | Enzym. | 10.2 | 20.4 | | 19.7 | 25.2 | n.d. | 28.1 | 243 |

*nmol/g fresh weight basis unless stated otherwise; [a]µg/g; [b]nmol/mg chlorophyll; [c]mg C/dm$^2$; [d]Basis unstated; [e]µmol/m$^2$; [f]nnmol/plant part; [g]Dry weight basis; [h]nmol/mL; [i]1,3-DPGA; [j]µmol/g; [k]conc., m*M*; [l]µmol/mg protein; [m]Percentage by weight; [n]Including 2-PGA.

*Continued*

**Table 1-5** Triose Phosphates in Plants*—cont'd

| No. | Plant part | Method | G3P | DHAP | TP | α-GP | 2-PGA | 3-PGA | DPGA | PEP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Centaurea moschata* L. (Sweet Sultan) | | | | | | | | | | | |
| 1 | Leaf[a] | PC/PC | | | | | | | | 1740 | 244 |
| *Chloris gayana* Kunth. (Rhodes Grass) | | | | | | | | | | | |
| 1 | Leaf | Enzym. | | | | | | 2800 | | 140 | 245 |
| *Cicer arietinum* L. (Chickpea) | | | | | | | | | | | |
| 1 | Seed | Enzym. | | | | | | | <100 | | 246 |
| 1 | 48-h seedling, cotyledon[d,f] | Enzym. | 5.2 | 34.5 | | | | | | 41.7 | 247 |
| 1 | –, embryonic axis[d,f] | Enzym. | 1.2 | 9.2 | | | | | | 4.2 | 247 |
| *Citrus sinensis* L. (Orange) | | | | | | | | | | | |
| 1 | Fruit juice[d] | IEC | | + | | + | | + | + | + | 248 |
| *Coriandrum sativum* L. (Coriander) | | | | | | | | | | | |
| 1 | Leaf[b] | Enzym. | | 88.8 | | | | | | | 249 |
| *Cucumis sativus* L. (Cucumber) | | | | | | | | | | | |
| 1 | Leaf | IEC | | | | | | 144 | | | 250 |
| *Cucurbita maxima* Duch. (Hubbard Squash) | | | | | | | | | | | |
| 1 | Sieve tube exudate | TLC/TLC | | | | | | + | | | 240 |
| 1 | Ripe fruit exudate[d,h] | Enzym. | 12 | 31 | | | 69 | 253 | | 243 | 251 |
| 1 | Seedling cotyledon | Enzym. | | | 46 | | 37 | 235 | | 111 | 252 |
| *Cucurbita pepo* L. (Pumpkin) | | | | | | | | | | | |
| 1 | Stem exudate[d,h] | Enzym. | 38 | 47 | | | 71 | 277 | | 104 | 251 |
| 1 | Unripe fruit exudate[d,h] | Enzym. | 15 | 20 | | | 27 | 112 | | 36 | 251 |
| *Daucus carota* L. (Carrot) | | | | | | | | | | | |
| 1 | Root | Enzym. | | 2.5 | | | | 28 | | | 253 |
| 1 | Root | Enzym. | | | 10.4 | | | | | | 254 |
| *Distichlis spicata* (L.) Greene (Coastal Saltgrass) | | | | | | | | | | | |
| 1 | Leaf | GLC | | | | 420 | | | | | 255 |
| *Erythronium japonicum* Decne (Katakuri) | | | | | | | | | | | |
| 1 | Leaf[e] | Enzym. | | | | | | 102.8 | | | 256 |
| *Fagopyrum esculentum* L. (Buckwheat) | | | | | | | | | | | |
| 1 | Seedling | Enzym. | | 3 | | 30 | | 25 | | 8 | 257 |
| *Fragaria* spp. (Strawberry) | | | | | | | | | | | |
| 1 | Leaf | Enzym. | | 5.5 | | | | 27.5 | | | 258 |
| 1 | Leaf | Enzym. | | | | | | 22.9 | | | 259 |
| *Glycine max* (L.) Merr. (Soybean) | | | | | | | | | | | |
| 1 | Seed | Enzym. | | | | | | | | 2.8 | 260 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Leaf[d,e] | Enzym. | | | 26 | | | 123 | | | 261 |
| 1 | Seedling | Enzym. | | | 85 | | | | | | 262 |
| *Gossypium barbadense* L. (Sea Island Cotton) | | | | | | | | | | | |
| 1 | Leaf[a] | PC/PC | | | | | | 2.25 | | | 263 |
| *Gossypium hirsutum* L. (Upland Cotton) | | | | | | | | | | | |
| 1 | Leaf, glandless | Enzym. | | | | | | 570 | | | 264 |
| *Helianthus annuus* L. (Sunflower) | | | | | | | | | | | |
| 1 | Leaf[e] | Enzym. | | 14.2 | | | | 85.5 | | | 239 |
| *Helianthus tuberosus* L. (Jerusalem Artichoke) | | | | | | | | | | | |
| 1 | Tuber | Enzym. | | | | | | 101 | | 23.8 | 265 |
| *Hemerocallis* hybrid (Daylily) | | | | | | | | | | | |
| 1 | Flower petal | TLC/TLC | | | | + | | + | | + | 266 |
| *Hordeum distichon* Alef. ssp. *nutans* (Two-Rowed Barley) | | | | | | | | | | | |
| 1 | Sprout | Enzym. | 1800 | 13,500 | | | | | | | 267 |
| *Hordeum vulgare* L. (Barley) | | | | | | | | | | | |
| 1 | Leaf[b,d] | Enzym. | | | 16 | | 6 | 102 | | 19 | 268 |
| 1 | Leaf[b,d] | Enzym. | | 24 | | | | | 333 | | 269 |
| 1 | Leaf[b,d] | Enzym. | | | | 35 | | | | | 270 |
| 1 | Leaf[b,d] | Enzym. | | | | | | 367 | | | 271 |
| 1 | –, stroma[b,d] | Enzym. | | | | | | 217 | | | 271 |
| 1 | –, cytosol[b,d] | Enzym. | | | | | | 151 | | | 271 |
| 1 | –, vacuole[b,d] | Enzym. | | | | | | 0 | | | 271 |
| 2 | Seedling | TLC/TLC | | | | | | + | | + | 272 |
| *Kalanchoe blossfeldiana* v. Poelln. (Flaming Katy) | | | | | | | | | | | |
| 1 | Leaf[g] | Enzym. | | | 60 | | 50 | 50 | | 200 | 273 |
| *Kalanchoë daigremontiana* Ham. and Per. (Devil's Backbone) | | | | | | | | | | | |
| 1 | Leaf | Enzym. | | | 8.5 | | | 16.5 | | 26.5 | 274 |
| 1 | Leaf[b] | Enzym. | | | | | | 355 | | 70 | 275 |
| *Lactuca sativa* L. (Lettuce) | | | | | | | | | | | |
| 1 | Seed[g] | Enzym. | | | | | | | | 80 | 276 |
| *Lens culinaris* Medik. (Lentil) | | | | | | | | | | | |
| 1 | Seed | Enzym. | | | | | | | <100 | | 246 |
| 1 | Sprout | Enzym. | | | | | | | <500 | | 246 |
| *Lycopersicon esculentum* Mill. (Tomato) | | | | | | | | | | | |
| 1 | Leaf | Enzym. | | | | | | 25 | | | 277 |
| 1 | Fruit | Enzym. | | | 7.5 | | | | | 14 | 278 |
| 1 | Green fruit | Enzym. | | | | | | | | 17.5 | 258 |

*nmol/g fresh weight basis unless stated otherwise; [a]μg/g; [b]nmol/mg chlorophyll; [c]mg C/dm$^2$; [d]Basis unstated; [e]μmol/m$^2$; [f]nnmol/plant part; [g]Dry weight basis; [h]nmol/mL; [i]1,3-DPGA; [j]μmol/g; [k]conc., m*M*; [l]μmol/mg protein; [m]Percentage by weight; [n]Including 2-PGA.

*Continued*

**Table 1-5** Triose Phosphates in Plants*—cont'd

| No. | Plant part | Method | G3P | DHAP | TP | α-GP | 2-PGA | 3-PGA | DPGA | PEP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Malus domestica* Borkh. (Apple) | | | | | | | | | | | |
| 1 | Fruit, immature | Enzym. | | 3 | | | | 11 | | 7.5 | 258 |
| 2 | Fruit, mature | Enzym. | | 2-3 | | | 1-2 | 7-10 | | 3-4 | 279 |
| *Malus sylvestris* (L.) Mill (Crabapple) | | | | | | | | | | | |
| 1 | Stem phloem tissue | PC/PC | | | | | | + | | | 227 |
| *Medicago sativa* L. (Alfalfa) | | | | | | | | | | | |
| 1 | Root | PC/PC | + | + | | | | + | | | 280 |
| 1 | Root nodule | Enzym. | | | | | | | | 160 | 281 |
| 1 | Shoot | PC/PC | + | + | | | | + | | | 280 |
| *Mucuna pruriens* (L.) D.C. (Cowitch Bean) | | | | | | | | | | | |
| 1 | Leaf[e] | Enzym. | | | 15 | | | 46 | | | 282 |
| *Musa cavendishii* Lam. ex Pax. (Dwarf Banana) | | | | | | | | | | | |
| 1 | Fruit[g] | Enzym. | | | 60 | | | | | | 283 |
| 1 | Fruit, green | Enzym. | | 6.5 | | | | | | 10 | 258 |
| *Nicotiana sylvestris* Speg. and Comes (Woodland Tobacco) | | | | | | | | | | | |
| 1 | Leaf[e] | Enzym. | | | | | | 214 | | | 284 |
| *Nicotiana tabacum* L. (Tobacco) | | | | | | | | | | | |
| 1 | Leaf | PC/PC | | | | + | | | | | 285 |
| 1 | Leaf[d,e] | Enzym. | | 35 | | | 21 | 153 | | 51 | 286 |
| 1 | –, mature | Enzym. | | | | | | | | 59.2 | 287 |
| 1 | –, senescent | Enzym. | | | | | | | | 16.9 | 287 |
| 1 | Shoot | Enzym. | | | | | | 23.4 | | | 288 |
| 1 | Root | Enzym. | | | | | | 13.4 | | | 288 |
| *Oryza sativa* L. (Rice) | | | | | | | | | | | |
| 1 | Grain[d] | Enzym. | n.d. | 85 | | | | 820 | | 180 | 289 |
| 1 | Grain, germ-free | Enzym. | | | | | | | 1000 | | 246 |
| 1 | –, germ | Enzym. | | | | | | | <100 | | 246 |
| *Panicum coloratum* Walt. (Kleingrass) | | | | | | | | | | | |
| 1 | Leaf | Enzym. | | | | | | | | 400 | 7 |
| *Persea americana* Mill. (Avocado) | | | | | | | | | | | |
| 1 | Fruit, mesocarp[h] | Enzym. | 33 | | | | 23 | 17 | 17[i] | 32 | 290 |
| *Phaseolus vulgaris* (L.) Banks (Common Beans) | | | | | | | | | | | |
| 1 | Bean | Enzym. | | | | | | | <100 | | 246 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Leaf | IEC | | | | | 1360 | | | | 22 |
| 1 | Leaf[d] | Enzym. | | | 1450 | | | 5200 | | | 291 |
| 1 | Seed cotyledon | $^{31}$P NMR | | | | + | | | | | 49 |
| *Phragmites communis* Trin. (Water Reed) | | | | | | | | | | | |
| 1 | Leaf[b] | PC/PC | | 10 | | | | 96 | | 0.010 | 292 |
| *Picea abies* (L.) Karst. (Norway Spruce) | | | | | | | | | | | |
| 1 | Needle (leaf)[b,g] | Enzym. | | | 910 | | | 640 | | | 293 |
| *Pisum sativum* L. (Peas) | | | | | | | | | | | |
| 1 | Leaf[b] | Enzym. | | 58.4 | | | | | | | 249 |
| 1 | Leaf chloroplast | HPLC | | | + | | | + | | | 106 |
| 1 | Root[d,j] | Enzym. | | | 10 | | | | | 19 | 294 |
| 1 | Seed | IEC | | | | | | 160 | | | 24 |
| 1 | Seed, round | Enzym. | | | 20 | | | | | | 295 |
| 1 | Seed, wrinkled | Enzym. | | | 55 | | | | | | 295 |
| 1 | Seed | Enzym. | | | | | | | <100 | | 246 |
| 1 | Seed | Enzym. | | 20 | | | 50 | 33 | | 112 | 296 |
| *Populus deltoides* Bartr. ex Marsh (Eastern Cottonwood) | | | | | | | | | | | |
| 1 | Leaf[b] | Enzym. | | | 30 | | | 190 | | | 297 |
| *Populus gelrica* (Houtz.) Houtz. | | | | | | | | | | | |
| 1 | Bark[d,k] | Enzym. | 0.004 | | | | | | | | 298 |
| *Populus nigra* L. (Black Poplar) | | | | | | | | | | | |
| 1 | Bark[d,k] | Enzym. | 0.003 | | | | | | | | 298 |
| *Portulaca grandiflora* Hook. (Rose Moss) | | | | | | | | | | | |
| 1 | Leaf[b] | PC/PC | | | | | | | | 0 | 244 |
| *Prunus armeniaca* L. (Apricot) | | | | | | | | | | | |
| 1 | Leaf | TLC/TLC | | | | | | + | | + | 37 |
| *Pyrus communis* L. (Pear) | | | | | | | | | | | |
| 1 | Fruit | Enzym. | | | + | | + | + | + | + | 299 |
| *Quercus rubra* L. (Red Oak) | | | | | | | | | | | |
| 1 | Leaf[e] | Enzym. | | | | Data not given | | | | | 282 |
| *Raphanus sativus* L. (Radish) | | | | | | | | | | | |
| 1 | Leaf | Enzym. | | | 42 | | | 95 | | | 300 |
| *Rhododendron ponticum* L. (Common Rhododendron) | | | | | | | | | | | |
| 1 | Detached leaf | Enzym. | | | | | | 54 | | 14 | 301 |
| *Ricinus communis* L. (Castor Bean) | | | | | | | | | | | |
| 1 | Seed, endosperm[d,f] | Enzym. | | 0.010 | | | | 0.070 | | 0.041 | 302 |

*nmol/g fresh weight basis unless stated otherwise; [a]μg/g; [b]nmol/mg chlorophyll; [c]mg C/dm$^2$; [d]Basis unstated; [e]μmol/m$^2$; [f]nnmol/plant part; [g]Dry weight basis; [h]nmol/mL; [i]1,3-DPGA; [j]μmol/g; [k]conc., m*M*; [l]μmol/mg protein; [m]Percentage by weight; [n]Including 2-PGA.

*Continued*

**Table 1-5** Triose Phosphates in Plants*—cont'd

| No. | Plant part | Method | G3P | DHAP | TP | α-GP | 2-PGA | 3-PGA | DPGA | PEP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Seedling, cotyledon | Enzym. | | | 14.3 | | 76 | 680 | | 315 | 303 |
| 1 | –, hypocotyl | Enzym. | | | 18 | | | 25 | | 4 | 304 |
| 1 | –, phloem exudate[h] | Enzym. | | | 62 | | | 63 | | 23 | 304 |
| *Saccharum officinarum* L. (Sugarcane) | | | | | | | | | | | |
| 1 | Leaf | Enzym. | | | | | | | | 820 | 305 |
| 1 | Leaf | PC/PC | | | | | | + | | + | 306 |
| 1 | Root | PC/PC | | | | | | + | | + | 306 |
| 1 | Stalk, third internode[l] | Enzym. | | | 10.3 | | | | | 6.3 | 307 |
| | | and variation from third to ninth internode | | | | | | | | | |
| *Saccharum officinarum* × *S. spontaneum* × *S. barberi* | | | | | | | | | | | |
| 1 | Leaf[e] | Enzym. | | | 63 | | | 171 | | 94 | 308 |
| *Saccharum sinense* Roxb. | | | | | | | | | | | |
| 1 | Leaf[f] | Enzym. | | | | | | | | 59 | 305 |
| *Salix triandra* L. (Almond Willow) | | | | | | | | | | | |
| 1 | Phloem exudate | TLC/TLC | | | | | | + | | tr | 309 |
| *Sesamum alatum* Thonn. | | | | | | | | | | | |
| 1 | Leaf[c] | Enzym. | | | 50.7 | | | 208.5 | | | 310 |
| *Sesasum indicum* L. (Sesame) | | | | | | | | | | | |
| 1 | Leaf[c] | Enzym. | | | 42.8 | | | 185.6 | | | 310 |
| 1 | Leaf | Enzym. | | | 19 | | | 230 | | | 311 |
| 1 | –, stroma[b] | Enzym. | | 8 | | | | 81 | | | 312 |
| *Solanum tuberosum* L. (Potato) | | | | | | | | | | | |
| 1 | Tuber[g,m] | LePage | | | 0.37 | | | | | | 13 |
| 14 | Tuber | PC/PC | | | | | | + | | | 313 |
| 1 | Tuber[d] | PC/PC | | | 2.5 | 2.2 | | 12[n] | | 1.5 | 314 |
| 1 | Tuber | PC | | | | + | | + | | | 315 |
| 1 | Tuber | IEC | | | | | | 147 | | | 316 |
| 1 | Tuber | Enzym. | | | | | | | <500 | | 246 |
| 1 | Tuber | Enzym. | | | 4.7 | | | | | | 317 |
| 1 | Mature tuber | Enzym. | | 1.5 | | | | 25 | | 13 | 258 |
| 1 | –, cytosol[b] | Enzym. | | 8 | | | | 22 | | | 312 |
| 1 | Tuber | Enzym. | | 6 | | | 12 | 40 | | 24 | 318 |
| | | and variation in TP, 3-PGA, and PEP levels along the stolon-apex axis | | | | | | | | | 319 |
| *Sorghum bicolor* (L.) Moench (Sorghum) | | | | | | | | | | | |
| 1 | Leaf[b] | Enzym. | | 150 | | | | | | 250 | 320 |
| 1 | Leaf | GLC | | | | 700 | | | | | 255 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Spartina alterniflora* Lois. (Smooth Cordgrass) | | | | | | | | | | |
| 1 | Leaf | GLC | | | 1480 | | | | | 255 |
| *Spinacia oleracea* L. (Spinach) | | | | | | | | | | |
| 1 | Root[d,j] | Enzym. | | 13 | | | | | 26 | 294 |
| 1 | Leaf | PC/PC | | | | | + | + | | 321 |
| 1 | Leaf | $^{31}$P NMR | + | | 0.5 | | + | | + | 50 |
| 1 | Leaf[b] | Enzym. | | 35 | | 13 | 500 | | 31 | 322 |
| 1 | Leaf[b,d] | Enzym. | | 35 | | | 373 | | 26 | 323 |
| 1 | Leaf[b,d] | Enzym. | | | 32 | | | | | 270 |
| 1 | Leaf[b,d] | Enzym. | ~ 20 | | | | | | | 324 |
| 1 | –, stroma[b,d] | Enzym. | 16 | | | | 268 | | | 325 |
| 1 | –, cytosol[b,d] | Enzym. | 6 | | | | 66 | | | 325 |
| 1 | Leaf chloroplast[b,d] | IEC | | 2.94 | | | | 70.9 | | 20 |
| 1 | Leaf, protoplast[b] | Enzym. | | 44.3 | | | 89.7 | | | 326 |
| 1 | –, chloroplast[b] | Enzym. | | 17.4 | | | 64.6 | | | 326 |
| 1 | –, extrachloroplast[b] | Enzym. | | 33.4 | | | 17.0 | | | 326 |
| *Spirodela oligorrhiza* (Kurz.) Hegelm. (Duckweed) | | | | | | | | | | |
| 1 | Whole plant | PC/PC | | 15 | 15 | | 230 | | 37 | 327 |
| *Tilia platyphyllos* Scop. (Large-Leaved Linden) | | | | | | | | | | |
| 1 | Phloem exudate | TLC/TLC | | | | | + | | + | 328 |
| *Trifolium subterraneum* L. (Sub Clover) | | | | | | | | | | |
| 1 | Whole plant | IEC | | | | | 2570 | | | 329 |
| 1 | Seed germ | Enzym. | | | | | | <500 | | 246 |
| 1 | 6-day root[g] | Enzym. | 6.7 | 29 | | | | | | 330 |
| 1 | 6-day shoot[g] | Enzym. | 1.6 | 37 | | | | | | 330 |
| *Triticum aestivum* L. (Wheat) | | | | | | | | | | |
| 1 | Root[d,j] | Enzym. | | 39 | | | | | 13 | 294 |
| 1 | Seed[g] | Enzym. | 2.6 | 35.1 | | | | | | 330 |
| 1 | 10-day leaf | PC/PE | + | | | | + | | + | 331 |
| 1 | 10-day leaf | TLC/TLE | | | | | + | | + | 331 |
| 1 | Leaf[b,d] | Enzym. | | 30 | | | 752 | | 34 | 323 |
| 1 | Leaf | GLC | n.d.(< 10) | | | | | | | 255 |
| *Vicia faba* L. (Broad Bean) | | | | | | | | | | |
| 1 | Leaf | PC/PC | | | | | + | + | | 321 |
| *Vigna mungo* (L.) Hepper (Black Gram) | | | | | | | | | | |
| 1 | 4-day seedling, hypocotyl tip | Enzym. | 0.8 | 1.0 | | | | | | 332 |
| *Vigna radiata* (L.) Wilcz. (Mung Bean) | | | | | | | | | | |
| 1 | Seedling | Enzym. | | 96 | | | | | | 262 |
| 1 | Leaf[c] | Enzym. | 60.2 | | | | | | | 249 |

*nmol/g fresh weight basis unless stated otherwise; [a]μg/g; [b]nmol/mg chlorophyll; [c]mg C/dm$^2$; [d]Basis unstated; [e]μmol/m$^2$; [f]nnmol/plant part; [g]Dry weight basis; [h]nmol/mL; [i]1,3-DPGA; [j]μmol/g; [k]conc., m*M*; [l]μmol/mg protein; [m]Percentage by weight; [n]Including 2-PGA.

*Continued*

**Table 1-5** Triose Phosphates in Plants*—cont'd

| No. | Plant part | Method | G3P | DHAP | TP | α-GP | 2-PGA | 3-PGA | DPGA | PEP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Vitis vinifera* L. (Wine Grape) | | | | | | | | | | | |
| 1 | Seedless berry | Enzym. | | | 7 | | | | | 11 | 333 |
| 1 | Fruit, juice | Enzym. | | 0 | | | | | | | 334 |
| 1 | Leaf | Enzym. | 3-PGA/TP ratio unchanged during 4 AM-6 PM photoperiod | | | | | | | | 335 |
| *Xanthium strumarium* L. (Cocklebur) | | | | | | | | | | | |
| 1 | Leaf[b,d] | Enzym. | | | 32 | | | 280 | | | 336 |
| *Yucca flaccida* Haw (Weak-Leaf Yucca) | | | | | | | | | | | |
| 1 | Phloem exudate | TLC/TLC | | | | | | + | | + | 309 |
| *Zea mays* L. (Corn) | | | | | | | | | | | |
| 1 | Leaf[b] | PC/PE | | 45 | | | | 185 | | 49.5 | 337 |
| 1 | Leaf[b,d] | Enzym. | | 234 | | | | 429 | | 59 | 338 |
| 1 | Leaf[b,d] | Enzym. | | | 233 | | | 341 | | 51 | 339 |
| 1 | –, midrib[b] | Enzym. | | | 417 | | | | | 104 | 340 |
| 1 | –, lamina[b] | Enzym. | | | 350 | | | | | 116 | 340 |
| 1 | Leaf, chloroplast[b] | Enzym. | | | 131 | | | 461 | | | 341 |
| 1 | –, cytosol[b] | Enzym. | | | 279 | | | 349 | | | 341 |
| 1 | –, vacuole[b] | Enzym. | | | 12 | | | 5 | | | 341 |
| 1 | Grain, endosperm[g] | Enzym. | 0.8 | 1.3 | | | | 20.7 | | 3.2 | 342 |
| 1 | –, starch granule[g] | Enzym. | 0.06 | 0.4 | | | | 1.6 | | 0.7 | 342 |
| 1 | –, germ | Enzym. | | | | | | | <100 | | 246 |
| 1 | Flower, ovary[h] | Enzym. | | | | | | 28 | | | 343 |
| 1 | Root | PC/PC | + | | | | | | | + | 12 |
| 1 | Root | TLC/TLC | + | | | | | | | + | 12 |

*nmol/g fresh weight basis unless stated otherwise.
[a]μg/g.
[b]nmol/mg chlorophyll.
[c]mg C/dm$^2$.
[d]Basis unstated.
[e]μmol/m$^2$.
[f]nnmol/plant part.
[g]Dry weight basis.
[h]nmol/mL.
[i]1,3-DPGA.
[j]μmol/g.
[k]conc., m*M*.
[l]μmol/mg protein.
[m]Percentage by weight.
[n]Including 2-PGA

consecutively, together with F6P and F1,6P, in a single metabolically related sequence (Fig. 1-2):

> *DHAP was assayed in the presence of 60 μmoles of tris-chloride, pH 7.6; 0.2 μmole of NADH in 20 mM EDTA and sample. The reaction, in a total volume of 1.04 ml, was started by the addition of 20 IU of α-glycerophosphate dehydrogenase. After completion, [G3P] was assayed by the addition of 60 IU of triose-P isomerase.*
>
> Steer, B. T., "Control of Diurnal Variations in Photosynthetic Products. I. Carbon Metabolism", *Plant Physiol.* **1974** *54*(5), 758–761,[242] reprinted by permission of the American Society of Plant Biologists, © 1974.

G3P and DHAP are often assayed together as triose phosphate (TP) using a mixture of α-GP dehydrogenase and TP isomerase in the procedure above. To assay α-GP, the procedure is reversed (Table 1-3, reaction 3). α-GP is oxidized to DHAP by NAD in the presence of α-GP dehydrogenase and hydrazine; the amount of α-GP is measured by the increase in absorbance of NADH at 340 nm. PEP, 2-PGA, and 3-PGA may also be analyzed consecutively in reactions coupled to the oxidation of NADH to NAD (Table 1-3, reaction 5).

> *Pyruvate was assayed using a reaction mixture containing 60 mmoles of tris-chloride [buffer], pH 7.6; 60 mmoles of KCl; 0.1 mmole of $MnSO_4$; 0.2 mmole of ADP; 0.2 mmole of 2,3-diphosphoglycerate; 0.2 mmole of NADH in 20 mM EDTA and sample. The reaction was started by adding 86 IU of lactic dehydrogenase and recording changes in absorbance at 340 nm. The total volume was 1.13 ml. The PEP, 2PGA, and 3PGA were determined sequentially by adding 37 IU of pyruvate kinase, 13 IU of enolase, and 5 IU of phosphoglycerate mutase, respectively.*
>
> Steer, B. T., "Control of Diurnal Variations in Photosynthetic Products. I. Carbon Metabolism", *Plant Physiol.* **1974** *54*(5), 758–761,[242] reprinted by permission of the American Society of Plant Biologists, © 1974.

An alternative sequence for 3-PGA, preferred by some because two moles of NADH are oxidized per mole of 3-PGA, involves a two-step reduction of 3-PGA to α-GP via G3P and DHAP (Table 1-3, reactions 2 and 4).

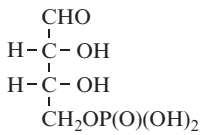
## 1,3-DPGA and 2,3-DPGA

The record on these substances in plants is sparse. An unidentified DPGA was detected in extracts of spinach and broad bean leaves by two-dimensional PC[321] and in extracts of $^{32}$P-labeled maize roots by one-dimensional PC.[344] 1,3-DPGA, a Calvin cycle metabolite, has been detected in Bartlett pear fruit[299] but not in *C. roseus* suspension cells.[243] 2,3-DPGA, a cofactor for PGA mutase, has been detected in orange juice[248] and quantitated in a variety of plant extracts.[246] Both substances were assayed by enzymatic methods: 1,3-DPGA by oxidation to G3P with NADH in the presence of G3P dehydrogenase (Table 1-3,

reaction 4), and 2,3-DPGA by a colorimetric method based on its stimulation of PGA mutase (Fig. 1-2, step 11).

## Tetrose Phosphates

This group is represented by a single aldose phosphate, E4P.



D-Erythrose 4-Phosphate (E4P), $C_4H_9O_7P$; Beilstein **1**, $E_{IV}$ 4175. *(R*,R*)-2,3-Dihydroxy-4-(phosphonooxy)butanal* [1961].

### Occurrence

E4P is a metabolite of the photosynthetic carbon reduction cycle (Calvin cycle) of higher plants (Fig. 1-3). In step 1, F6P transfers a two-carbon ketol segment to G3P, forming E4P and Xu5P. In step 2, the E4P thus formed undergoes an aldol condensation with another molecule of G3P, giving Se1,7P. These reactions occur within the chloroplast, found only in the green leaf. E4P is also a metabolite of the oxidative pentose phosphate pathway. In step 3, Se7P transfers a three-carbon ketol segment to G3P, forming E4P and F6P. In step 4, the E4P undergoes a similar reaction with Xu5P, forming F6P and G3P. These reactions take place in the cytoplasm, and in the chloroplast during periods of darkness. E4P is required for

**FIGURE 1-3 Tetrose Phosphates.** (1, 4) Transketolase [E.C. 2.2.1.1], TPP, $Mg^{2+}$. (2,5) Aldolase [E.C. 4.1.2.13]. (3,6) Transaldolase [E.C. 2.2.1.2].

the synthesis of shikimic acid, a precursor of the phenolics and the aromatic amino acids.

### Physical Properties

D-Erythrose 4-Phosphate

E4P [R.N. 19234-99-2; see also 585-18-2]: $[\alpha]_D$ +0.5°[30]; $\Delta G^\circ$ −142.7 kcal/mol.[84] Spectra: $^1$H NMR (fig.),[97] $^{13}$C NMR,[345] $^{31}$P NMR (fig.)[97]; GC-MS.[96] Chromatography: PC,[346] TLC,[347] GC,[143] IEC,[347] HPLC.[106] Electrophoresis: TLE,[105] zone.[88] E4P is over 90%

**Table 1-6** Tetrose Phosphates in Plants*

| No. | Plant part | E4P | References |
|---|---|---|---|
| *Populus gelrica* (Houtz.) Houtz. | | | |
| 1 | Bark[a,b] | 0.003 | 298 |
| *Populus nigra* L. (Black Poplar) | | | |
| 1 | Bark[a,b] | 0.020 | 298 |
| *Vigna mungo* (L.) Hepper (Black Gram) | | | |
| 1 | 4-day seedling, hypocotyl tip | 2.3 | 332 |

*nmol/g fresh weight basis unless stated otherwise.
[a]Conc., m*M*.
[b]Basis unstated.

hydrated (to the *gem*-diol) in aqueous solution.[348] It tends to dimerize during evaporation.[349]
$K_2C_4H_7O_7P$: $[\alpha]_D$ −4.7°.[30]

### Synthesis

E4P may be prepared (a) by phosphorylation of 2,3-di-*O*-benzoyl-D-erythrose dimethyl acetal with diphenyl phosphorochloridate[350] or (b) by cleavage of G6P with lead tetraacetate.[349] It is best stored as the penultimate products of synthesis: dimethyl acetal cyclohexylamine salt[350] or hydrazide barium salt.[349]

### Hydrolysis

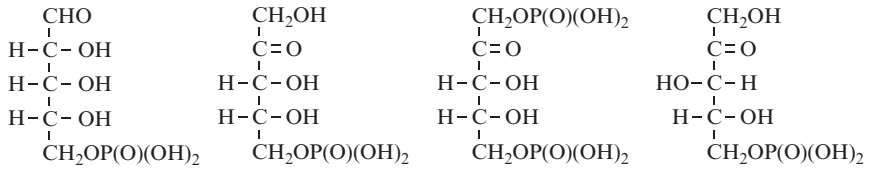
E4P is rapidly hydrolyzed by 1*N* NaOH at room temperature,[350] but is stable to 0.1*N* HCl and to buffers of pH 3 to 5 at 37 °C.[351] Its half-life in 1*N* $H_2SO_4$ at 100 °C is 20 min.[350]

### Analysis

The estimation of E4P is based on enzymatic methods. In the presence of F6P, E4P is converted quantitatively by transaldolase to Se7P and G3P (Fig. 1-3, reaction 6) and assayed either as G3P (Table 1-3, reaction 1)[298] or as DHAP (Table 1-3, reaction 2)[332] by measuring the change in optical density at 340 nm.

## Pentose Phosphates

This group comprises one aldose phosphate (R5P) and three ketose phosphates (Ru5P, Ru1,5P, and Xu5P).




D-Ribose 5-Phosphate (R5P), $C_5H_{11}O_8P$; Beilstein **1**, H 859, $E_I$ 434, $E_{IV}$ 4245, **31**, 21. *D-Ribose 5-(Dihydrogen Phosphate)* [1953].

D-Ribulose 5-Phosphate (Ru5P) $C_5H_{11}O_8P$; not listed in Beilstein. *D*-erythro-*2-Pentulose 5-(Dihydrogen Phosphate)* [1956].

D-Ribulose 1,5-Bisphosphate (Ru1,5P), $C_5H_{12}O_{11}P_2$; not listed in Beilstein. *D*-erythro-*2-Pentulose 1,5-Bis(dihydrogen Phosphate)* [1963].

D-Xylulose 5-Phosphate (Xu5P), $C_5H_{11}O_8P$; not listed in Beilstein. *D*-threo-*2-Pentulose 5-(Dihydrogen Phosphate)* [1977].

## Occurrence

R5P, Ru5P, Ru1,5P, and Xu5P are metabolites of the photosynthetic carbon reduction cycle (Calvin cycle) of higher plants (Fig. 1-4, reading clockwise). In steps 1 and 2, F6P or Se7P transfer a two-carbon ketol segment to G3P, forming E4P (or R5P) and Xu5P. In step 3, R5P is converted to its isomer Ru5P. In step 4, Ru5P is phosphorylated by ATP, completing the cycle and regenerating Ru1,5P for further $CO_2$ fixation (step 5). In step 6, Xu5P is converted to its epimer Ru5P by the enzyme Ru5P 3-epimerase. All of these reactions occur within the chloroplast, found only in the green leaf.

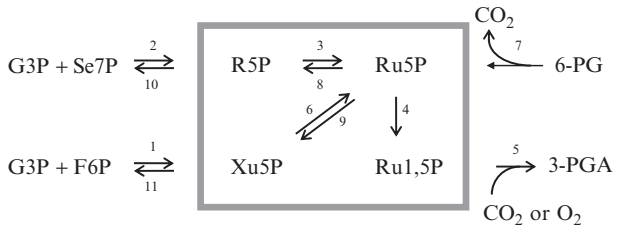



**FIGURE 1-4 Pentose Phosphates**. (1, 2) Transketolase [E.C. 2.2.1.1]. (3) R5P isomerase [E.C. 5.3.1.6]. (4) Ru5P kinase [E.C. 2.7.1.19], ATP. (5) Ru1,5P carboxylase-oxygenase [Rubisco, E.C. 4.1.1.39], $CO_2$ or $O_2$, $H_2O$, $Mg^{2+}$. (6) Ru5P epimerase [E.C. 5.1.3.1]. (7) 6-PG dehydrogenase [E.C. 1.1.1.44], NADP.

R5P, Ru5P, and Xu5P are also metabolites of the pentose phosphate respiratory pathway (Fig. 1-4, reading counterclockwise). In step 7, 6-PG is oxidized by NADP, giving Ru5P, NADPH, and $CO_2$. In steps 8 and 9, Ru5P is converted to its isomer R5P and epimer Xu5P, respectively. In step 10, R5P and Xu5P interact to form Se7P and G3P. In step 11, Xu5P interacts with E4P to form F6P and G3P. These reactions all take place in the leaf cytoplasm outside any organelle and in chloroplasts in periods of darkness.

## Physical Properties

D-Ribose 5-Phosphate

R5P [R.N. 4300-28-1; see also 3615-55-2]: White powder,[345] $[\alpha]_D^{20}$ +22.8° (0.2*N* HCl)[352]; p$K_a$ 6.24,[353] 13.05 (thermometric, 25 °C)[354]; conformation[355]; heat of ionization ($\Delta H°$, $\Delta S°$).[354] Spectra: Far-UV (fig.),[356] FTIR,[357] Raman (fig.),[358] GC-MS,[96] $^1$H NMR (fig.),[359] $^{13}$C NMR (fig.),[85] $^{31}$P NMR (fig.).[360] Chromatography: PC,[9,32] TLC,[105] GC,[143] IEC,[85,361] HPLC,[26,144] IC.[107] Electrophoresis: PE,[32] TLE,[105] zone,[88] CZE,[136] CE,[90] isotachophoresis.[88]

$Na_2C_5H_9O_8P$ [R.N. 18265-46-8]: Colorless hygroscopic solid,[360] $[\alpha]_D^{22}$ +14.8° ($H_2O$).[362]

$BaC_5H_9O_8P{\cdot}5H_2O$ [R.N. 15673-79-7]: Monoclinic,[363] colorless hexagonal plates,[364] d 2.05,[363] $[\alpha]_D^{26}$ +5.99° ($H_2O$).[364] Spectra: Far-UV (fig.),[365] X-ray.[363]

D-Ribulose 5-Phosphate

Ru5P [R.N. 551-85-9; see also 4151-19-3]: $[\alpha]_D^{20}$ −40° (0.2*N* HCl)[352] $\Delta G°$ −179.6 kcal/mol.[84] Spectra: UV,[366] CD,[366] ORD,[366] GC-MS,[96] $^{13}$C NMR (fig.),[85] $^{31}$P NMR.[68] Chromatography: PC,[367] TLC,[105] IEC,[352,361] HPLC,[368] HPLC-MS-MS.[100] Electrophoresis: PE,[367] TLE,[105] zone,[88] isotachophoresis.[88]

$Li_2C_5H_9O_8P$: White nonhygroscopic powder.[369]

$BaC_5H_9O_8P$: Precipitate, sol. $H_2O$, insol. EtOH.[352]

D-Ribulose 1,5-Bisphosphate

Ru1,5P [R.N. 24218-00-6; see also 2002-28-0]: Spectra: UV (fig.),[370] IR (fig.),[103] GC/MS,[96] $^1$H NMR (fig.),[103] $^{13}$C NMR (fig.),[85] $^{31}$P NMR.[68] Chromatography: PC,[9] TLC,[33] IEC,[371] HPLC,[26,144] IC (fig.).[107] Electrophoresis: PE,[9] TLE,[105] zone,[88] CE,[90] isotachophoresis.[88]

$Ba_2C_5H_8O_{11}P_2$ [R.N. 82130-67-4]: Solid, sol. $H_2O$, insol. EtOH.[371] Stable for months at −20 °C but isomerizes to xylulose 1,5-bisphosphate if stored at room temperature.[372]

D-Xylulose 5-Phosphate

Xu5P [R.N.4212-65-1; see also 28848-87-5]: Pale yellow syrup, $[\alpha]_D^{25}$ −6.5° ($H_2O$),[373] $\Delta G°$ −179.6 kcal/mol.[84] Spectra: UV,[366] $^1$H NMR,[373] $^{13}$C NMR,[374] GC-MS.[96] Chromatography: PC,[367] IEC.[375] Electrophoresis: PE.[367]

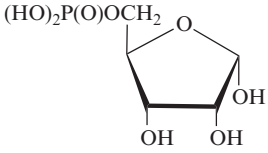
## Synthesis

R5P may be prepared (a) by phosphorylation of methyl 2,3-isopropylidene-β-D-ribofuranoside with $POCl_3$/pyridine[364] or dibenzyl phosphorochloridate,[376] (b) by acid-catalyzed hydrolysis of AMP with Dowex 50 at 100 °C,[377] or (c) by enzymatic phosphorylation of D-ribose with ribokinase and ATP.[360] The relative merits of these methods has been discussed.[360] Ru5P may be prepared (a) by enzymatic phosphorylation of D-ribulose with isomerase-free ribulokinase and ATP,[378] (b) by isomerization of R5P with R5P isomerase,[25] or (c) by oxidation of 6-PG with crystalline 6PG dehydrogenase.[369] Ru1,5P may be prepared (a) by phosphorylation of R5P with phosphoribulokinase and ATP in the presence of phosphoriboisomerase[371] or (b) by the combined action of four immobilized enzymes on G6P.[360] Xu5P may be prepared (a) by enzymatic phosphorylation

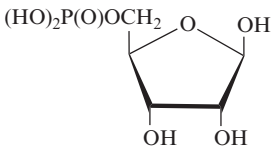
of D-xylulose with xylulokinase and ATP,[379] (b) by isomerization of Ru5P with 3-epimerase,[380] or (c) by transketolase-catalyzed condensation of hydroxypyruvate with G3P.[25]

## Structure

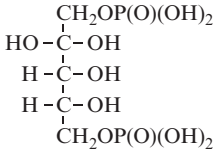
An aqueous solution of R5P at pH 5.5 contains predominantly α-furanose (**5**, 35.6%) and β-furanose (**6**, 63.9%) forms, with only 0.1% free aldehyde and 0.5% *gem*-diol. The rates of ring-opening at pH 7.5 and 40 °C are 100 and 40 $s^{-1}$, respectively, and are catalyzed by acid below pH 2 and by base above pH 7[348]:




**5**, R.N. 34980-65-9




**6**, R.N. 34980-66-0




**7**

Aqueous solutions of Ru1,5P contain 12% (NMR)[85] to 16% (IR)[103] of *gem*-diol **7** in addition to the free ketose. Ru5P solutions also appear to contain predominantly free ketose.[85] Ru1,5P tends to isomerize to Xu1,5P when exposed to solutions of pH > 8.[360]

Xu5P is unstable in buffer solutions in the pH 5.3-8.4 range[381]; aqueous solutions should be maintained at pH 5.0 or below to avoid isomerization.[382]

## Hydrolysis

Hydrolysis of $R_5P$ with 0.01*N* HCl at 100 °C liberated 73.2% of the P after 28 h[364]; its half-life in 0.1*N* NaOH at 22 °C was about 20 h.[377] For the effect of pH over the range 1.5-12 on the hydrolysis of R5P at 100 °C, see Dimroth *et al.*[205]

Ru5P is less stable to acid than R5P; its half-life in 1*N* $H_2SO_4$ at 100 °C is about 60 min.[352] Ru5P is unstable above pH 7.[381] Calorimetric measurements gave $\Delta H^\circ$ −5.69 kJ/mol (enthalpy) and $\Delta C^\circ_P$ −63 J/(mol K) (heat capacity) for the hydrolysis of R5P with alkaline phosphatase. The corresponding data for Ru5P were −12.43 kJ/mol and −84 J/(mol K), respectively.[383]

The hydrolysis of Ru1,5P with 1*N* $H_2SO_4$ at 100 °C is first order with no change in slope, indicating that the two phosphate groups are equally labile. The half-life is 20 min.[371] Hydrolysis in 1*N* NaOH is also first-order ($t_{1/2}$ 2.8 min)[371] but only one phosphate group is labile.[384] The $C_1$ phosphate group is lost by β-elimination, followed by further degradation.[385] For the kinetics of hydrolysis over the pH 2.0-13.0 range, see Haga *et al.*[384]

## Phosphorylation

Phosphorylation of R5P with phosphoric acid/DCC in the presence of pyridine gives D-ribose-5-di- and -triphosphate, separated by IEC in yields of 20-25% and 10%, respectively.[386]

**Table 1-7** Pentose Phosphates in Plants*

| No. | Plant part | Method | R5P | Ru5P | Ru1,5P | Xu5P | References |
|---|---|---|---|---|---|---|---|
| *Amaranthus caudatus* L. (Love-Lies-Bleeding) | | | | | | | |
| 1 | Leaf[a,b] | Enzym. | | | 70 | | 224 |
| *Arbutus unedo* L. (Strawberry Tree) | | | | | | | |
| 1 | Leaf[a,b] | Enzym. | | | 91 | | 229 |
| *Beta vulgaris* L. Sugar Beet | | | | | | | |
| 1 | Leaf[a,b] | Enzym. | | | 140 | | 236 |
| *Brassica campestris* L. (Turnip Rape) | | | | | | | |
| 1 | Pod, deseeded | Enzym. | | | 3148 | | 238 |
| *Brassica napus* L. (Rape) | | | | | | | |
| 1 | Leaf[c] | Enzym. | | | 41.6 | | 239 |
| *Erythronium japonicum* Decne. (Katakuri) | | | | | | | |
| 1 | Leaf[c] | Enzym. | | | 10.3 | | 256 |
| *Glycine max* (L.) Merr. (Soybean) | | | | | | | |
| 1 | Leaf[a,c] | Enzym. | 80[d] | | 57 | | 389 |
| 1 | Leaf[b] | HPLC | + | | 210 | | 26 |
| *Gossypium hirsutum* L. (Upland Cotton) | | | | | | | |
| 1 | Leaf, glandless | Enzym. | | | 210 | | 264 |
| *Helianthus annuus* L. (Sunflower) | | | | | | | |
| 1 | Leaf[c] | Enzym. | | | 54.3 | | 239 |
| *Hordeum vulgare* L. Barley | | | | | | | |
| 1 | Leaf[a,b] | Enzym. | | | 63 | | 269 |
| 2 | Seedling | TLC/TLC | | | + | | 272 |
| *Kalanchoë daigremontiana* Ham. and Perr. (Devil's Backbone) | | | | | | | |
| 1 | Leaf[b] | Enzym. | | | 50 | | 275 |
| *Lycopersicon esculentum* Mill. (Tomato) | | | | | | | |
| 1 | Leaf[b] | Enzym. | | | 165 | | 390 |
| *Mucuna pruriens* (L.) DC (Cowitch Bean) | | | | | | | |
| 1 | Leaf[c] | Enzym. | | | 22 | | 282 |
| *Nicotiana sylvestris* Speg. and Comes (Woodland Tobacco) | | | | | | | |
| 1 | Leaf[c] | Enzym. | | | 21 | | 284 |
| *Phaseolus vulgaris* L. Beans | | | | | | | |
| 1 | Leaf[a] | Enzym. | | | 800 | | 291 |
| *Phragmites communis* Trin. (Water Reed) | | | | | | | |
| 1 | Leaf[b] | PC/PC | | | 12 | | 292 |
| *Pisum sativum* L. (Peas) | | | | | | | |
| 1 | Leaf chloroplast | HPLC | | | + | | 106 |
| *Populus gelrica* (Houtz.) Houtz. | | | | | | | |
| 1 | Bark[a,e] | Enzym. | 0 | | | | 298 |
| *Populus nigra* (Black Poplar) | | | | | | | |
| 1 | Bark[a,e] | Enzym. | 0.017 | | | | 298 |
| *Pyrus communis* L. (Pear) | | | | | | | |
| 1 | Fruit skin | IEC | + | | | | 19 |
| *Quercus rubra* L. Red Oak | | | | | | | |
| 1 | Leaf[c] | Data not given | | | | | 282 |
| *Raphanus sativus* L. (Radish) | | | | | | | |
| 1 | Leaf[a,c] | Enzym. | | | 92 | | 11 |

**Table 1-7** Pentose Phosphates in Plants*—cont'd

| No. | Plant part | Method | R5P | Ru5P | Ru1,5P | Xu5P | References |
|---|---|---|---|---|---|---|---|
| *Secale cereale* L. (Rye) | | | | | | | |
| 1 | Leaf chloroplast, diploid[f] | Enzym. | 48.0 | | | | 391 |
| 1 | –, tetraploid[f] | Enzym. | 34.9 | | | | 391 |
| *Solanum tuberosum* L. (Potato) | | | | | | | |
| 1 | Tuber | PC/PC | + | | | | 392 |
| *Spinacia oleracea* L. (Spinach) | | | | | | | |
| 1 | Leaf | PC/PC | | | + | | 321 |
| 1 | Leaf[a,b] | Enzym. | | | 77.2 | | 393 |
| 1 | –, stroma[a,b] | Enzym. | | | 183 | | 325 |
| 1 | –, chloroplast[a,b] | IEC | 1.08 | | 9.43 | | 20 |
| 1 | Leaf protoplast[b] | Enzym. | | | 21.5 | | 326 |
| 1 | –, chloroplast[b] | Enzym. | | | 21.9 | | 326 |
| 1 | –, extrachloroplast[b] | Enzym. | | | 0 | | 326 |
| *Triticum aestivum* L. (Wheat) | | | | | | | |
| 1 | Leaf[a,b] | Enzym. | | | 50 | | 387 |
| 1 | 10-day leaf | PC/PE | + | | | | 331 |
| *Triticum durum* Desf. (Durum Wheat) | | | | | | | |
| 1 | Leaf[b] | Enzym. | | | 333 | | 394 |
| *Vicia faba* L. (Broad Bean) | | | | | | | |
| 1 | Leaf | PC/PC | | | + | | 321 |
| *Vigna mungo* (L.) Hepper (Black Gram) | | | | | | | |
| 1 | 4-day seedling, hypocotyl tip | Enzym. | 5.8 | 0.9 | | 1.4 | 332 |
| *Xanthium strumarium* L. (Cocklebur) | | | | | | | |
| 1 | Leaf[a,b] | Enzym. | | | 100-120 | | 395 |
| *Zea mays* L. (Corn) | | | | | | | |
| 1 | Leaf[b] | PC/PC | | | 11.4 | | 337 |
| 1 | Leaf[a,b] | Enzym. | | | 56 | | 338 |

*nmol/g fresh weight basis unless stated otherwise.
[a]Basis unstated.
[b]nmol/mg chlorophyll.
[c]µmol $m^2$.
[d]Including Ru5P.
[e]Conc., m*M*.
[f]µg/g.

## Separation and Analysis

R5P and Ru1,5P can be separated from other phosphate esters by IEC, by HPLC, or by two-dimensional PC, TLC, or PC/PE after extraction with perchloric acid or trichloroacetic acid. Quantitative data were reported for Ru1,5P in some cases. These methods are applicable in principle to the pentulose phosphates Ru5P and Xu5P, but Table 1-7 shows neither.

### Analysis Without Separation

*(1) Enzymatic Method*

The pentose phosphates may be determined by enzymatic reactions coupled to either the oxidation of G3P to 3-PGA by NAD (Table 1-3, reaction 1) or the reduction of 1,3-DPGA to G3P by NADH (Table 1-3, reaction 4). In either case, the amount of pentose phosphate is calculated from the change in optical density of the NAD(H) at 340 nm.

The first method (oxidation) was used for the determination of R5P in poplar bark[298] and for the sequential determination of R5P, Ru5P, and Xu5P in *Vigna mungo* seedlings.[332] The second method (reduction) was used for the determination of Ru1,5P in turnip rape,[238] velvet bean,[282] red oak,[282] wheat,[387] corn,[338] and cotton.[264]

A radiometric method based on the following reaction, introduced by Latzko and Gibbs[388] in 1969, has become the method of choice for the determination of Ru1,5P in plant extracts because it employs a single enzyme (Rubisco) instead of three, and is capable of measuring pools of 1 n*M* or less[5b]:

$$\mathrm{Ru1,5P} + {}^{14}\mathrm{CO_2} + \mathrm{H_2O} \overset{\text{Rubisco}}{\rightarrow} 3-\mathrm{PGA} + \left[{}^{14}\mathrm{C}\right]3-\mathrm{PGA}$$

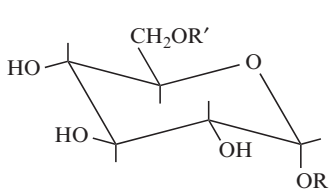
> *Ribulose-1,5-bisphosphate was determined by $^{14}C$ incorporation into PGA using purified RuBP carboxylase [E.C. 4.1.1.39]. . . . Assays were run in 300 ml total volume (100 mM N,N-bis(2-hydroxyethyl)glycine [Bicine], pH 8.0, 20 mM $MgCl_2$, 13 mM [$^{14}C$]$NaHCO_3$ [40-50 Bq $nmol^{-1}$], 50 mg carboxylase) with 100 ml of sample per assay. Duplicate assays were run for 30 min at room temperature; the reactions were terminated by adding 0.2 ml 2*N *formic acid. The samples were dried in an air stream and counted by liquid scintillation spectrometry.*
>
> Badger, M. R.; Sharkey, T. D.; von Caemmerer, S., "The Relationship between Steady-State Gas Exchange of Bean Leaves and the Levels of Carbon-Reduction-Cycle Intermediates", *Planta* **1984**, *160*(4), 306–315,[291] reprinted by permission of Springer, © 1984.

R5P, Ru5P, and Xu5P could also be determined by the $^{14}CO_2$ method with the aid of the appropriate enzymes,[5b] but this method has not yet been applied to the higher plants.

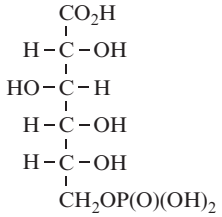
## Hexose Phosphates

This large group comprises primarily the 1- and 6-phosphates of glucose and fructose and to a lesser extent the corresponding mannose and galactose phosphates. The glucose phosphates (G1P, G6P, and G1,6P), including reduced glucose phosphates (So1P and So6P) and oxidized glucose phosphates (6-GP and its lactones), are considered first:

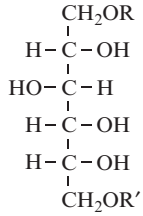
### Glucose Phosphates




**G1P**, R′ = H, R = $P(O)(OH)_2$
**G6P**, R = H, R′ = $P(O)(OH)_2$
**G1,6P**, R = R′ = $P(O)(OH)_2$




**6-PG**




**So1P**, R′ = H, R = $P(O)(OH)_2$
**So6P**, R = H, R′ = $P(O)(OH)_2$

D-Glucose 1-Phosphate (G1P), $C_6H_{13}O_9P$; not listed in Beilstein. Cori ester, *α-D-Glucopyranose 1-(Dihydrogen Phosphate)* [1944].

D-Glucose 6-Phosphate (G6P), $C_6H_{13}O_9P$; Beilstein **1**, $E_{IV}$ 4381. Robison ester, *D-Glucose 6-(Dihydrogen Phosphate)* [1949].

D-Glucose 1,6-Bisphosphate (G1,6P), $C_6H_{14}O_{12}P_2$; not listed in Beilstein. *α-D-Glucopyranose 1,6-Bis(dihydrogen Phosphate)* [1963].

D-6-Phosphogluconic Acid (6-PG), $C_6H_{13}O_{10}P$; Beilstein **3**, $E_{III}$ 1063, $E_{IV}$ 1258. *D-Gluconic Acid 6-(Dihydrogen Phosphate)* [1963].

Sorbitol 1-Phosphate (So1P), $C_6H_{15}O_9P$: not listed in Beilstein. *D-Glucitol 1-(Dihydrogen Phosphate)* [1978].

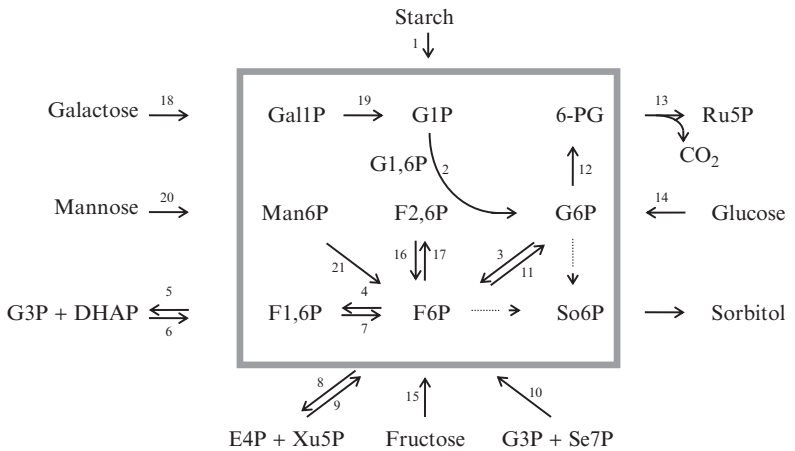



**FIGURE 1-5 Hexose Phosphates.** (1) Starch phosphorylase [E.C. 2.4.1.1], $H_2PO_4^-$. (2) Phosphoglucomutase [E.C. 2.7.5.1], G1,6P, $Mg^{2+}$. (3,11) Phosphoglucose isomerase [E.C. 5.3.1.9]. (4,15) Phosphofructokinase [PFK, E.C. 2.7.1.11], ATP, $Mg^{2+}$. (5,6) F1,6P aldolase [E.C. 4.1.2.13]. (7) Fructose 1,6-bisphosphatase [E.C. 3.1.3.11]. (8,9) Transketolase [E.C. 2.2.1.1]. (10) Transaldolase [E.C. 2.2.1.2]. (12) G6P dehydrogenase [E.C. 1.1.1.49], NADP. (13) 6-PG dehydrogenase [E.C. 1.1.1.44], NADP. (14,20) Hexokinase [E.C. 2.7.1.1], ATP, $Mg^{2+}$. (16) F6P 2-kinase [E.C. 2.7.1.105], ATP. (17) Fructose 2,6-bisphosphatase [E.C. 3.1.3.46]. (18) Galactokinase [E.C. 2.7.1.6], ATP. (19) Gal1P uridyltransferase [E.C. 2.7.7.10], UDPG. (21) Man6P isomerase [E.C. 5.3.1.8].

Sorbitol 6-Phosphate (So6P), $C_6H_{15}O_9P$: Beilstein **1**, $E_{IV}$ 2849. *D-Glucitol 6-(Dihydrogen Phosphate)* [1977].

## Occurrence

G1P and G6P are metabolites of the Embden-Meyerhof-Parnas glycolysis pathway, a sequence common to all of the higher plants (Fig. 1-5). G1P, formed from starch by the action of starch phosphorylase (step 1), is converted to G6P by phosphoglucomutase (step 2). The next step is the isomerization of G6P to F6P (step 3). These reactions take place in the cytoplasm outside any organelle. G6P and 6-PG are also metabolites of the hexose monophosphate shunt, a part of the pentose phosphate respiratory pathway in which G6P is oxidized via 6-PG lactone to 6-PG (step 12) and then to Ru5P with the loss of $CO_2$ (step 13). These reactions take place in the cytoplasm and (during periods of darkness) in chloroplasts. G6P is also formed from glucose by phosphorylation with ATP (step 14) and from F6P by the action of G6P isomerase (step 11).

G1,6P is a required cofactor for phosphoglucomutase [E.C. 2.7.5.1], the enzyme that catalyzes the G1P ↔ G6P interconversion (step 2). Animal tissues contain enzymes that are capable of synthesizing and degrading G1,6P, but it is not known if these enzymes are present in plants.[396]

Some plants produce sorbitol rather than sucrose as their major product of photosynthesis. So1P and So6P have both been shown to be present in apricot (*Prunus armeniaca* L.) leaf in almost equal amounts (0.0064 and 0.0072 mmol/g fwb, respectively).[397] Sorbitol phosphate was also detected in *Cotoneaster dammeri*.[37] So6P is probably formed from G6P or F6P by enzymatic reduction, but So1P is an anomaly.

## Physical Properties

Glucose 1-Phosphate

G1P [59-56-3; see also 6866-69-9]: $[\alpha]_D^{25}$ +120° ($H_2O$),[398] p$K_a$ 1.1[398] and 6.504[399]; $\Delta G°$ −5 kcal/mol[142]; dissociation constant ($\Delta G°$, $\Delta H°$, $\Delta S°$)[399]; countercurrent distribution[141]; MO calc.[166,400] Spectra: Far-UV (fig.),[401] ORD,[402] GC/MS,[96] HPLC-MS-MS,[100] ESI-MS-MS,[403] FAB-MS-MS,[404] $^1$H NMR (fig.),[131] $^{13}$C NMR,[405] $^{31}$P NMR,[68], ESR.[406] Chromatography: PC,[9,32] TLC,[36] IEC,[86,134] HPTLC,[407] GC,[408] HPLC,[26] IC.[107] Electrophoresis: PE,[32] TLE,[36] CZE.[136]

$Na_2C_6H_{11}O_9P{\cdot}3.5H_2O$ [R.N. 32972-46-6; see also 56401-20-8]: Monoclinic cryst., d 1.74[409]; diamagnetic susceptibility $\chi_M$ $-135 \times 10^{-6}$ cm$^3$/mol at 25 °C.[410] Spectra: $^1$H, $^{23}$Na, and $^{31}$P NMR,[411] LD-MS,[412] X-ray.[409]

$KC_6H_{12}O_9P$ [R.N. 53823-71-5; see also 105751-36-8]: Colorless orthorhombic prisms, d 1.81. Spectra: X-ray.[413]

$K_2C_6H_{11}O_9P{\cdot}2H_2O$ [R.N. 5996-14-5; see also 6736-77-2, 89705-70-4]: Fine needles, $[\alpha]_D^{26}$ +78° ($H_2O$),[414] d 1.85[415]; heat of combustion $Q_M$ 2761 kJ/mol.[416] Spectra: IR (fig.),[417] $^{13}$C and $^{31}$P NMR (figs.),[418] X-ray.[415,419]

$CaC_6H_{11}O_9P$ [R.N. 6997-09-7]: Dissociation constants ($\Delta G°$, $\Delta H°$, $\Delta S°$).[420]

$BaC_6H_{11}O_9P{\cdot}3H_2O$ [R.N. 71662-16-3]: White, nonhygroscopic powder, easily sol. $H_2O$, insol. EtOH, $[\alpha]_D^{25}$ +75°.[398]
$(C_6H_{11}NH_2)_2C_6H_{13}O_9P$ [R.N. 90357-92-9]: Cryst., mp 163-169 °C dec., $[\alpha]_D^{25}$ +64.0° ($H_2O$).[421] Spectra: $^1H$, $^{13}C$, and $^{31}P$ NMR.[422]
$(C_{23}H_{26}N_2O_4)_2C_6H_{13}O_9P$ (brucine salt): Colorless needles, mp 182-184 °C dec., $[\alpha]_{589}^{27} + 0.5°(H_2O)$.[423]

Glucose 6-Phosphate

G6P [R.N. 56-73-5]: Amorphous, nonhygroscopic white powder,[424] $[\alpha]_{546}^{20} + 41.4°(H_2O)$,[425] p$K_a$ 1.50, 6.22,[426] 11.71 (thermometric, 25 °C)[354]; countercurrent distribution[141]; redox potential[427]; MO calc.[166] Spectra: UV,[94] far-UV (fig.),[401] IR (fig.),[94] CD,[94,102] ORD,[402] GC/MS,[96] ESR (fig.),[406] $^1H$ NMR,[131] $^7C$ NMR,[345] $^{31}P$ NMR.[68] Chromatography: PC,[9,32] TLC,[36] IEC,[86,134] GC,[408] HPLC,[26,428] IC (fig.).[107] Electrophoresis: PE,[32] TLE,[36] zone,[88] CZE,[89] CE,[90] isotachophoresis.[88]
$Li_2C_6H_{11}O_9P$ [R.N. 52888-21-8]: $[\alpha]_D^{20}$ +22.5° ($H_2O$).[429]
$NaC_6H_{12}O_9P$ [R.N. 54010-71-8]: Monoclinic needles, d 1.83. Spectra: X-ray.[430]
$Na_2C_6H_{11}O_9P{\cdot}2H_2O$ [R.N. 3671-99-6; see also 111283-45-5]: Diamagnetic susceptibility $\chi_M$ $-135 \times 10^{-6}$ cm$^3$/mol at 25 °C.[410] Spectra: FD-MS.[431]
$K_2C_6H_{11}O_9P$ [R.N. 5996-17-8]: mp 95-97 °C dec.,[432] $[\alpha]_D^{24}$ +21.2° ($H_2O$), readily sol. $H_2O$.[433]
$BaC_6H_{11}O_9P{\cdot}7H_2O$ [R.N. 5996-16-7]: Monoclinic cryst., mp 157 °C dec.,[432] $[\alpha]_D^{25}$ +17.4° ($H_2O$),[434] d 2.09[435]; solubility in water, 0.002 mol/L at 25 °C, 0.001 mol/L at 0 °C.[436] Spectra: X-ray.[435]
$(C_{23}H_{26}N_2O_4)_2C_6H_{13}O_9P$ (brucine salt): Colorless needles, mp 182-184 °C, $[\alpha]_{589}^{27} + 0.5°(H_2O)$.[423]

Glucose 1,6-Bisphosphate

G1,6P [R.N. 305-58-8; see also 10139-18-1]: Spectra: $^1H$ NMR (fig.).[437] Chromatography: PC,[438] TLC,[105] IEC,[86] HPLC.[161] Electrophoresis: PE,[439] TLE,[105] CE.[90]
$Na_4C_6H_{10}O_{12}P_2$: $[\alpha]_D^{28}$ +83.0° ($H_2O$).[440]
$Ba_2C_6H_{10}O_{12}P_2{\cdot}H_2O$: Precipitate.[440]
$(C_6H_{11}NH_2)_4C_6H_{14}O_{12}P_2{\cdot}4H_2O$: Cryst., $[\alpha]_D^{20}$ +31.0° ($H_2O$).[439]
$(C_{23}H_{26}N_2O_4)_4C_6H_{14}O_{12}P_2$ (brucine salt): Elongated prisms, dec. 185 °C, $[\alpha]_D^{26}$ −16.3° ($H_2O$).[440]

6-Phosphogluconic Acid

6-PG [R.N. 921-62-0; see also 2464-13-3]: $[\alpha]_{546}^{21}0°(H_2O)$.[425] Spectra: GC/MS,[96] $^{13}C$ NMR (fig.),[441] $^{31}P$ NMR.[68] Chromatography: PC,[9,32] TLC,[33] IC (fig.),[107] HPLC.[442] Electrophoresis: PE,[32] zone,[88] isotachophoresis.[88]
$Na_3C_6H_{10}O_{10}P$: Colorless, granular solid, $[\alpha]_D^{25}$ +1.9° ($H_2O$).[443] Dihydrate [R.N. 53411-70-4]: Monoclinic cryst., d 1.86; X-ray.[444]
$BaC_6H_{11}O_{10}P$: $[\alpha]_{546}^{21} + 0.2°(H_2O)$.[425]

$Ba_3(C_6H_{10}O_{10}P)_2$: $[\alpha]_{546}^{21} - 1.5^\circ (H_2O)$; solubility in $H_2O$, 7.1 g/L at 100 °C.[425]
$(C_{23}H_{26}N_2O_4)_3C_6H_{13}O_{10}P$ (brucine salt): Needles, $[\alpha]_D^{25}$ −29.9° ($H_2O$).[443]
γ-Lactone [R.N. 97323-75-6]: $[\alpha]_{546}^{21} + 21^\circ (0.1N HCl)$.[425] Spectra: $^{13}C$ and $^{31}P$ NMR.[445] Chromatography: GC.[446]
δ-Lactone [R.N. 2641-81-8]: Standard transformed Gibbs energy of formation ($\Delta_f G'^\circ$).[447] Spectra: $^{13}C$ and $^{31}P$ NMR.[445]

Sorbitol 1-Phosphate
So1P [R.N. 67670-70-6]: Spectra: GC/MS.[397] Chromatography: IEC, PC, TLC, GC.[397] Electrophoresis: TLE.[397]

Sorbitol 6-Phosphate
So6P [R.N. 20479-58-7]: Standard transformed Gibbs energy of formation ($\Delta_f G'^\circ$).[447] Spectra: GC/MS.[96] Chromatography: IEC,[448] PC,[448] TLC,[449] GC.[449] Electrophoresis: TLE.[449]
$BaC_6H_{13}O_9P$: Cryst.[450]

## Synthesis

G1P may be prepared (a) by phosphorylation of tetraacetylglucosyl-1-bromide with $Ag_3PO_4$[398] or silver diphenyl phosphate[414] or of 2,3,4,6-tetraacetyl-D-glucose with dibenzyl *N*,*N*-diethylphosphoramidite,[451] (b) by the reaction of β-D-glucose pentaacetate[452] or MOP β-D-glucopyranoside[422] with anhydrous phosphoric acid, or (c) by enzymatic hydrolysis of starch with potato phosphorylase in pH 6.7 phosphate buffer.[453]

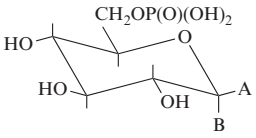
G6P may be prepared (a) by phosphorylation of glucose with polyphosphoric acid[454] or metaphosphoric acid,[424] (b) by phosphorylation of glucose,[432] methyl α-D-glucopyranoside,[429] or $O^1$,$O^2$-isopropylidene-α-D-glucofuranose[434] with $POCl_3$, (c) by phosphorylation of $O^1$,$O^2$,$O^3$,$O^4$-tetraacetyl-β-D-glucopyranose with diphenyl phosphorochloridate[433] or bis(2,4-dichlorophenyl) phosphorochloridite[455] or of $O^1$,$O^2$-isopropylidene-α-D-glucofuranose with dibenzyl phosphorochloridate,[456] or (d) by fermentation of glucose[425] or sucrose[457] with yeast. It can also be prepared enzymatically (e) by the action of phosphoglucomutase on G1P[458] or of hexose-phosphate isomerase on F6P.[436]

G1,6P may be prepared (a) by phosphorylation of $O^2$,$O^3$,$O^4$-triacetyl-$O^6$-(diphenylphosphono)glucosyl bromide with $Ag_3PO_4$ or silver diphenyl phosphate,[440] (b) by the reaction of tetraacetyl β-D-glucose 6-phosphate with anhydrous phosphoric acid,[438,439] or (c) by fermentation of sucrose with yeast.[459] 6-GP may be prepared (a) by oxidation of G6P with bromine[425] or iodine[443] or by enzymatic oxidation of G6P with G6P dehydrogenase. The use of immobilized enzymes is advantageous.[460] So1P and So6P may be prepared by borohydride reduction of F1P[397] and F6P,[448,450] respectively.

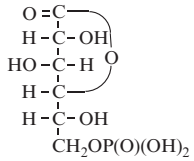
## Structure

The preferred conformation of the pyranose ring of G1P in aqueous solution is $^4C_1$ with the $C_5$—$C_6$ bond in gg ↔ tg equilibrium.[461] G6P solutions contain no free aldehyde (<0.4%)[94]; the bulk of the G6P is a mixture of α (**8**) and β (**9**) pyranose anomers in 38.5:61.5 ratio.[462]

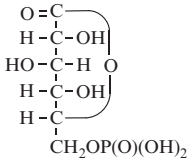
The rate of interconversion of the anomers is 0.0658 $s^{-1}$ (α to β) and 0.0389 $s^{-1}$ (β to α).[463] The interconversion is catalyzed by G6P 1-epimerase.




**8**, A = H, B = OH [R.N. 1520911-7]
**9**, A = OH, B = H [R.N. 15209-12-8]




**10**




**11**

6-PG cyclizes spontaneously to D-gluconolactone 6-phosphate as observed by the change in optical rotation over a 4-h period.[425,443] The product, like that of D-gluconic acid itself, is the γ (1-4) lactone **10**. The initial product of enzymatic oxidation of G6P, however, is the δ (1-5) lactone **11**,[464] which is subsequently hydrolyzed to 6-PG by 6-PG lactonase. The rates of ring-opening hydrolysis of **10** and **11** at pH 7.4 and 34 °C were $3.98 \times 10^{-3}$ and $7.14 \times 10^{-3}$ $s^{-1}$, respectively, reflecting the greater stability of the γ-lactone.[465]

## Hydrolysis

G1P is stable to base but the rate of hydrolysis at 100 °C increases slowly from pH 8 to pH 4 and more rapidly at lower pH.[466] The rate was $0.288 \times 10^{-5}$ $s^{-1}$ at pH 7.46 and $161 \times 10^{-5}$ $s^{-1}$ at pH 2.5.[467] This is interpreted as a normal rate for the monoanion $AH^-$ and an abnormal rate for the neutral acid $H_2A$ relative to simple monoalkyl phosphates. In strongly acidic media, there is a rapid acid-catalyzed reaction whose rate depends on the Hammett acidity function. This reaction, in contrast to enzymatic hydrolysis,[468] proceeds by C—O bond fission.[467] For further detailed studies, see the cited references.[469,470]

The behavior of G6P toward hydrolysis is similar to that of simple monoalkyl phosphates in the acid region (pH < 5.8) but differs in the alkaline region. At pH 4.0, where the monoanion $HA^-$ is predominant, the rate constant for hydrolysis at 100 °C is $2.0 \times 10^{-5}$ $s^{-1}$. At lower pH, the rate profile falls to about $0.5 \times 10^{-5}$ $s^{-1}$ (neutral acid, $H_2A$), then rises steeply at pH < 0 owing to acid catalysis. At pH 7, the rate increases to a second plateau (dianion, $A^{2-}$), then rises steeply above pH 9 owing the base-catalyzed hydrolysis. The kinetics have been studied in detail.[426,471] Calorimetric measurements gave $\Delta H^\circ$ 0.91 kJ/mol, $\Delta C_P^\circ$ −48 J/(mol K) for the hydrolysis of G6P by alkaline phosphatase.[383]

Hydrolysis of both G1P and G6P in the mildly acid to neutral region is catalyzed by molybdate,[204] Th(IV),[215] Ce(III), and other M(III) salts,[216] and by UV radiation.[217] Hydrolysis of G1,6P with 1*N* HCl at 100 °C for 30 min gives G6P and $P_i$.[439] The rate constant *k* in 1*N* $H_2SO_4$ at 30 °C is $1.31 \times 10^{-5}$ $s^{-1}$.[440] The rate of hydrolysis of 6-PG in 1*N* HCl at 100 °C falls from $1.02 \times 10^{-5}$ to $0.59 \times 10^{-5}$ $s^{-1}$, probably reflecting different rates for the free acid and its lactone.[472]

So6P is quite stable to hydrolysis. Less than 10% of the phosphorus is liberated by either 1*N* HCl or 0.1*N* NaOH after 1 h at 100 °C,[448] but So6P is readily hydrolyzed to sorbitol by wheat germ acid phosphatase.[397]

## Metal Ion Complexes

G6P forms 1:1 complexes with Mg(II) and Ca(II). Their stability constants have been reported.[221]

## Separation and Analysis

### *(1) LePage and Umbreit Method*

G1P and G6P appear together with other phosphate esters in the barium-soluble fraction (see p 2) of the TCA extract. G1P is measured by the amount of $P_i$ released in 7 min at 100 °C with 1*N* HCl correlated with an increase in reducing value, and G6P is measured by its reducing value corrected for those due to F6P and pentose phosphate. This method has been superseded by those which follow.

### *(2) Chromatographic Methods*

G1P and G6P can be separated from other phosphate esters by IEC or HPLC, but not from each other unless the mobile phase contains a borate gradient (pages 2,3). An HPLC procedure was developed for the analysis of G1P and G6P in potato tuber based on selective conversion to 6-PG by PG mutase and 6-PG dehydrogenase.[473] The detection of G1,6P and 6-PG in orange juice, based on retention time and behavior on mild hydrolysis, could not be confirmed.[248] 6-PG was, however, isolated from an extract of ladino clover leaf by reverse phase HPLC on a Brownlee column with water/acetonitrile/dicyclohexylamine (84.5:14.5:1) as the mobile phase and quantitated by GC/MS after derivatization with TMS.[474] All but So1P and So6P can be separated by two-dimensional PC, TLC, PC/PE, or TLC/TLE (Table 1-8). Quantitative data were reported in a few instances for G1P, G6P, and 6-PG. The identities and relative amounts of the two sorbitol phosphates were determined by GC/MS after conversion to the tri-methysilyl derivatives.[397]

## Analysis Without Separation

### *(1) $^{31}$P NMR Method*

G6P has been identified by high-field FT $^{31}$P NMR in a number of plant tissues and extracts, and 6-PG in a spinach leaf extract (Table 1-8). For further details, see p 5.

### *(2) Enzymatic Methods*

G6P may be determined by enzymatic oxidation to 6-PG by NADP in the presence of G6P dehydrogenase (Table 1-3, reaction 6). The amount of G6P is calculated from the change in optical density of the NADP at 340 nm.

**Table 1-8** Glucose and Fructose Phosphates in Plants*

| No. | Plant part | Method | G1P | G6P | G1,6P | 6-PG | F1P | F6P | F1,6P | F2,6P | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acer pseudoplatanus* L. (Sycamore Maple) | | | | | | | | | | | |
| 1 | Suspension cells | $^{31}$P NMR | | + | | | + | | | | 46 |
| *Actinidia deliciosa* Liang. and Ferg. (Kiwi) | | | | | | | | | | | |
| 3 | Fruit | Enzym. | 12.9 | 113.5 | | | | 34.8 | 1.5 | | 222 |
| 1 | Callus culture | Enzym. | | 105 | | | | | | | 475 |
| 1 | Callus culture | $^{31}$P NMR | | + | | | | | | | 475 |
| *Allium cepa* L. (Onion) | | | | | | | | | | | |
| 1 | Leaf[a,b] | Enzym. | | | | | | | | 1.0 | 476 |
| *Amaranthus caudatus* L. (Love-Lies-Bleeding) | | | | | | | | | | | |
| 1 | Leaf[a,b] | Enzym. | | 183 | | | | 85 | 24 | | 224 |
| *Amaryllis vittata* L'Her. (Amaryllis) | | | | | | | | | | | |
| 1 | Pollen[a] | Enzym. | | | | | | | 600 | | 226 |
| *Ananas comosus* (L.) Merr. (Pineapple) | | | | | | | | | | | |
| 1 | Leaf[a] | Enzym. | | | | | | | | + | 477 |
| 1 | Phylloides | Enzym. | | | | | | | | 5-13 | 478 |
| *Annona cherimola* Mill. (Cherimoya) | | | | | | | | | | | |
| 1 | Fruit, mesocarp | Enzym. | | | | | | 102 | 75 | 0.046 | 479 |
| *Arabidopsis thaliana* (L.) Heynh (Mouse-Ear Cress) | | | | | | | | | | | |
| 1 | Leaf[b] | Enzym. | 20 | 200 | 2.98 | | | 50 | | 0.52 | 480 |
| *Arbutus unedo* L. (Strawberry Tree) | | | | | | | | | | | |
| 1 | Leaf[a,b] | Enzym. | | 57 | | | | 42 | 6 | | 229 |
| *Arum maculatum* L. (Cuckoopint) | | | | | | | | | | | |
| 1 | Club | Enzym. | 22.3 | 210.4 | | | | 39.5 | 21.8 | | 230 |
| *Avena sativa* L. (Oats) | | | | | | | | | | | |
| 1 | Seed | Enzym. | | 0 | | | | | | –[c] | 232 |
| 1 | –, embryo[d] | LePage | 141 | | | | | 97 | 7 | | 14 |
| *Beta vulgaris* (L.) Banks (Sugar Beet) | | | | | | | | | | | |
| 1 | Root, stored | LePage | 50 | 490 | | | | 120 | 90 | | 15 |
| 1 | –, vegetating | LePage | 50 | 450 | | | | 160 | 80 | | 15 |
| 1 | Leaf | LePage | 70 | 630 | | | | 130 | 180 | | 15 |
| 1 | Petiole, parenchyma | LePage | | 970 | | | | 200 | | | 17 |
| 1 | –, fibrovascular bundle | LePage | | 250 | | | | 70 | | | 17 |
| 2 | Axis[a,e] | Enzym. | 3.5-6.0 | 6.0-9.0 | | | | 12.5-17.5 | | | 481 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Leaf[a,f] | Enzym. | 3.6 | 8.7 | | | 1.7 | 1.2 | 0.06 | 482 |
| 1 | Leaf | PC/PC | | + | | + | + | | 0.6 | 483 |
| 1 | Leaf | PC/PC | | | | | + | + | | 484 |
| *Brassica campestris* L. (Turnip Rape) | | | | | | | | | | |
| 1 | Pod, deseeded[b] | Enzym. | | 145 | | | 13.7 | 9.9 | 0.032 | 238 |
| *Brassica napus* L. (Rape) | | | | | | | | | | |
| 1 | Leaf[g] | Enzym. | | 51.7 | | | 24.3 | 1.8 | | 239 |
| *Brassica nigra* (L.) Koch (Black Mustard) | | | | | | | | | | |
| 1 | Suspension cells | Enzym. | | | | | | | 0.051 | 485 |
| *Brassica pekinensis* (Lour.) Rupr. (Pe-tsai) | | | | | | | | | | |
| 1 | Petiole, vascular bundle | PC/PC | + | + | | | + | | | 36 |
| 1 | Petiole, vascular bundle | TLC/TLC | + | + | | | + | | | 36 |
| 1 | Petiole, vascular bundle | TLC/TLE | + | + | | | + | | | 36 |
| *Brassica rapa* L. (Turnip Rape) | | | | | | | | | | |
| 1 | Vascular bundle | TLC/TLC | | + | | | + | | | 240 |
| –, var. *rapa* (DC) Metzg. (White Turnip) | | | | | | | | | | |
| 1 | Tuber | Enzym. | | | | 21.1 | | | | 486 |
| 1 | Tuber | PC | | | | + | | | | 486 |
| *Bryiphyllum tubiflorum* Harv. (Chandelier Plant) | | | | | | | | | | |
| 1 | Leaf | Enzym. | | | | | | | + | 477 |
| 1 | Phylloides | Enzym. | | | | | | | 0.1-4.0 | 478 |
| *Camellia japonica* L. (Camellia) | | | | | | | | | | |
| 1 | Pollen | Enzym. | | | | | 11 | 0 | 0.01 | 487 |
| *Camellia sinensis* L. (Tea) | | | | | | | | | | |
| 1 | Leaf | Enzym. | 6.3 | 0.7 | | | | | | 488 |
| –, var. *assamica* (Mast.) Kitam. (Assam Tea) | | | | | | | | | | |
| 1 | Leaf | Enzym. | 12.5 | | 2.0 | | | | | 488 |
| *Capsicum annuum* L. (Bell Pepper) | | | | | | | | | | |
| 1 | Seed pericarp | | | | | | | | 0.60 | 489 |
| 1 | Leaf | Enzym. | | | | | 226 | 130 | | 242 |
| 1 | –, tip | Enzym. | | | | | | | 3.6 | 490 |
| 1 | –, base | Enzym. | | | | | | | 7.8 | 490 |
| *Catharanthus roseus* (L.) G. Don (Madagascar Periwinkle) | | | | | | | | | | |
| 1 | Suspension cells | Enzym. | 34.5 | 337.1 | | | 58.2 | 31.8 | 0.04 | 243 |
| 1 | Suspension cells | $^{31}$P NMR | | + | | | + | | | 46 |

*nmol/g fresh weight basis unless stated otherwise; [a]Basis unstated; [b]nmol/mg chlorophyll; [c]Almost unmeasurable; [d]nmol/plant part; [e]nmol/axis; [f]nmol/mg protein; [g]µmol/m$^2$; [h]nmol/mL; [i]Dry weight basis; [j]mg C/dm$^2$; [k]mol/mol CABP binding site; [l]µmol/g; [m]µg/g; [n]µg/mm$^2$; [o]Incl. G1P; [p]µmol/mg protein; [q]Conc., m*M*.

*Continued*

**Table 1-8** Glucose and Fructose Phosphates in Plants*—cont'd

| No. | Plant part | Method | G1P | G6P | G1,6P | 6-PG | F1P | F6P | F1,6P | F2,6P | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Cicer arietinum* L. (Chickpea) | | | | | | | | | | | |
| 1 | Seedling, cotyledon[a,d] | Enzym. | | 138.8 | | | | 32.4 | 8.3 | | 247 |
| 1 | –, embryonic axis[a,d] | Enzym. | | 20.0 | | | | 8.7 | 0.5 | | 247 |
| 1 | Leaf exudate[h] | HPLC | | 8.33 | | | | | | | 491 |
| *Citrullus lanatus* (Thunb.) Mats. and Nakai (Watermelon) | | | | | | | | | | | |
| 1 | Cotyledon | Enzym. | | | | | | | | 0.025 | 492 |
| *Citrus acida* Roxb. (Citron) | | | | | | | | | | | |
| 1 | Mature fruit[i] | IEC | 0 | 440 | | | | 380 | 180 | | 493 |
| 1 | Immature fruit[i] | IEC | 550 | 720 | | | | 3000 | 480 | | 493 |
| *Citrus paradisi* Macf. (Grapefruit) | | | | | | | | | | | |
| 1 | Leaf | Enzym. | | | | | | | | 0.75 | 494 |
| 1 | Fruit juice sac | Enzym. | | | | | | | | 0.08 | 494 |
| *Citrus sinensis* (L.) Osbeck (Orange) | | | | | | | | | | | |
| 1 | Fruit juice | IEC | + | + | + | + | | + | + | | 248 |
| 1 | Fruit juice sac | Enzym. | | | | | | | | 0.16 | 494 |
| *Coriandrum sativum* L. (Coriander) | | | | | | | | | | | |
| 1 | Leaf[b] | Enzym. | | | | | | | 96.4 | 0.072 | 249 |
| *Cucumis sativus* L. (Cucumber) | | | | | | | | | | | |
| 1 | Leaf | IEC | 125.4 | 390.0 | | | | 113.1 | | | 250 |
| *Cucurbita maxima* Duch. (Hubbard Squash) | | | | | | | | | | | |
| 1 | Sieve tub exudate | TLC/TLC | + | + | | | | + | | | 240 |
| *Cucurbita pepo* L. (Pumpkin) | | | | | | | | | | | |
| 1 | Leaf[j] | Enzym. | | | | | | 46.7 | 5.4 | | 252 |
| 1 | Seedling cotyledon | Enzym. | | 2113 | | | | | | | 252 |
| 1 | Stem exudate[a,b] | Enzym. | 128 | 746 | | 97 | | 319 | 134 | | 251 |
| 1 | Unripe fruit exudate[a,b] | Enzym. | 41 | 221 | | 34 | | 89 | 37 | | 251 |
| 1 | Ripe fruit exudate[a,b] | Enzym. | 67 | 2459 | | 118 | | 434 | 25 | | 251 |
| *Daucus carota* L. (Carrot) | | | | | | | | | | | |
| 1 | Tuber[k] | IEC | 0.14 | 0.23 | | | | 0.16 | | | 23 |
| 1 | Root | Enzym. | | 111 | | | | | | 0.120 | 253 |
| 1 | Root | Enzym. | | | | | 19.5 | | | | 486 |
| 1 | Root | Enzym. | | | | | | 3.04 | 0.23 | 0.014 | 317 |
| 1 | Root | Enzym. | | | | | + | | | | 486 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Egeria densa* Planch. (Brazilian Waterweed) | | | | | | | | | | | |
| 1 | Leaf[l] | Enzym. | | 105 | | | | | | | 495 |
| *Fagopyrum esculentum* L. (Buckwheat) | | | | | | | | | | | |
| 1 | Seedling | Enzym. | | 120 | | 4 | | 15 | 3 | | 257 |
| *Fragaria vesca* L. (Woodland Strawberry) | | | | | | | | | | | |
| 1 | Leaf | Enzym. | 28 | 247 | 8.3 | | | 46 | 4.3 | | 259,488 |
| *Glycine max* (L.) Merr. (Soybean) | | | | | | | | | | | |
| 1 | Leaf[a] | Enzym. | 84 | 675 | | | | 126 | | 0.195 | 496 |
| 1 | Leaf[b] | HPLC | 31 | 307 | | | | 175 | 32 | | 26 |
| 1 | Suspension cells | $^{31}$P NMR | | + | | | | + | | | 46 |
| 1 | Seed, cotyledon | $^{31}$P NMR | | + | | | | + | | | 47 |
| 1 | Seedling | Enzym. | | 95 | 18 | | | 26 | 39 | 45 | 262 |
| 1 | Root tip[i] | Enzym. | | 7900 | | <300 | | <200 | | | 497 |
| *Gossypium barbadense* L. (Sea Island Cotton) | | | | | | | | | | | |
| 1 | Leaf[m] | PC/PC | 2.18 | | | | 0.89 | | | | 263 |
| *Gossypium hirsutum* L. (Upland Cotton) | | | | | | | | | | | |
| 1 | Leaf[b] | Enzym. | | $170 \times 10^3$ | | | | $100.3 \times 10^3$ | | | 498 |
| *Helianthus annuus* L. (Sunflower) | | | | | | | | | | | |
| 1 | Leaf[g] | Enzym. | | 103.7 | | | | 34.4 | 5.6 | | 239 |
| 1 | –, youngn | PC | | 0 | | | | 2160 | 1000 | | 499 |
| 1 | –, budding stage[m] | PC | | 0 | | | | 0 | 950 | | 499 |
| 1 | –, flowering stage[m] | PC | | 60 | | | | 260 | 4950 | | 499 |
| *Helianthus tuberosus* L. (Jerusalem Artichoke) | | | | | | | | | | | |
| 1 | Tuber | IEC | | + | | | + | + | + | | 500 |
| 1 | Tuber | Enzym. | | 133 | | | | 33 | | 1.2 | 265 |
| 1 | Young stolon | $^{31}$P NMR | | + | | | | | | | 45 |
| *Hemerocallis* hybrid (Daylily) | | | | | | | | | | | |
| 1 | Flower petal | TLC/TLC | + | + | | + | | + | | | 266 |
| *Heracleum sphondylium* L. (Hogweed) | | | | | | | | | | | |
| 1 | Leaf | Enzym. | | | | | | | | 0.105 | 501 |
| *Hordeum distichon* Alef. ssp. *nutans* | | | | | | | | | | | |
| 1 | Sprout[n] | Enzym. | 1.25 | 77.6 | | | | 37.5 | 3.2 | | 267 |
| *Hordeum vulgare* L. (Barley) | | | | | | | | | | | |
| 2 | Dehusked grain[a,d] | Enzym. | 2.6-2.8 | 37 | | | | 9.0-11.0 | | | 502 |
| 1 | Leaf[b] | Enzym. | 16 | 89 | 3.8 | | | | | | 396 |

*nmol/g fresh weight basis unless stated otherwise; [a]Basis unstated; [b]nmol/mg chlorophyll; [c]Almost unmeasurable; [d]nmol/plant part; [e]nmol/axis; [f]nmol/mg protein; [g]μmol/m$^2$; [h]nmol/mL; [i]Dry weight basis; [j]mg C/dm$^2$; [k]mol/mol CABP binding site; [l]μmol/g; [m]μg/g; [n]μg/mm$^2$; [o]Incl. G1P; [p]μmol/mg protein; [q]Conc., m*M*.

*Continued*

**Table 1-8** Glucose and Fructose Phosphates in Plants*—cont'd

| No. | Plant part | Method | G1P | G6P | G1,6P | 6-PG | F1P | F6P | F1,6P | F2,6P | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Leaf[a,b] | Enzym. | | | | | | 73 | 6 | 0.048 | 269 |
| 1 | –, tillering stage[m] | PC | | 0 | | | | 0 | 0 | | 499 |
| 1 | –, ear-forming stage[m] | PC | | 1450 | | | | 4620 | 1020 | | 499 |
| 2 | Seedling | TLC/TLC | + | + | | + | | + | + | | 272 |
| 1 | Root tip | $^{31}$P NMR | | + | | | | | | | 503 |
| *Impatiens balsamina* L. (Garden Balsam) | | | | | | | | | | | |
| 1 | Root tip[i] | Enzym. | | 4700 | | | | | | | 497 |
| *Kalanchoë blossfeldiana* v. Poelln. (Flaming Katy) | | | | | | | | | | | |
| 1 | Leaf[i] | Enzym. | | 120 | | | | 30 | 5 | | 273 |
| *Kalanchoë daigremontiana* Hammett et Perrier (Devil's Backbone) | | | | | | | | | | | |
| 1 | Leaf | Enzym. | | 73.7 | | 3.0 | | 9.8 | 54 | | 274 |
| 1 | Leaf[a] | Enzym. | | | | | | | | + | 477 |
| *Lactuca sativa* L. (Lettuce) | | | | | | | | | | | |
| 1 | Leaf | $^{31}$P NMR | | + | | | | + | | | 48 |
| *Larix decidua* Mill. (European Larch) | | | | | | | | | | | |
| 1 | Cambial sap | IEC/PC | | + | | | | | | | 504 |
| *Lathyrus sativus* L. (Grass Pea) | | | | | | | | | | | |
| 1 | Leaflet[m] | TLC/TLC | 312 | | 593 | | | | | | 505 |
| *Lolium temulentum* L. (Darnel) | | | | | | | | | | | |
| 1 | Leaf | Enzym. | | 160 | | | | 63 | | | 506 |
| 1 | Leaf[a,b] | Enzym. | | | | | | | | 0.100 | 507 |
| *Lotus corniculatus* L. (Birdsfoot Trefoil) | | | | | | | | | | | |
| 1 | Root | Enzym. | | 190.7 | | | | | | | 508 |
| *Lycopersicon esculentum* Mill. (Tomato) | | | | | | | | | | | |
| 1 | Green fruit | Enzym. | | 80 | | | | 15 | 0.3 | | 258 |
| 1 | Fruit | Enzym. | | 240 | | | | 5 | 20 | | 278 |
| 1 | Flower ovary[j,m] | LePage | 130 | 420 | | | | 150 | 360 | | 18 |
| *Malus domestica* Borkh. (Apple) | | | | | | | | | | | |
| 1 | Immature fruit | Enzym. | | 80 | | | | 10 | 1.4 | | 258 |
| 1 | Flower bud[l] | Enzym. | | 610 | | | | | | | 509 |
| 2 | Mature fruit | Enzym. | | 22-25 | | | | 4-5 | 1 | | 279 |
| *Medicago sativa* L. (Alfalfa) | | | | | | | | | | | |
| 1 | Root | PC/PC | | + | | | | + | + | | 280 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 1 | Shoot | PC/PC | | + | + | + | | 280 |
| 1 | Root | Enzym. | | 122.1 | | | | 508 |
| 1 | –, nodule | Enzym. | | 1040 | 700 | 160 | | 281 |
| *Mesembryanthemum crystallinum* L. (Ice Plant) | | | | | | | | |
| 1 | Leaf[m] | Enzym. | | 32 | 8 | 1 | 0.08 | 510 |
| *Mucuna pruriens* (L.) D.C. (Cowitch Bean) | | | | | | | | |
| 1 | Leaf[g] | Enzym. | | 21 | 15 | 4.4 | | 282 |
| *Musa cavendishii* Pax. (Dwarf Banana) | | | | | | | | |
| 1 | Green fruit | Enzym. | | 70 | 15 | 0.5 | | 258 |
| 1 | Fruit[a] | Enzym. | | | | | 0.25 | 511 |
| *Nicotiana tabacum* L. (Tobacco) | | | | | | | | |
| 1 | Leaf[a,g] | Enzym. | 56 | 413 | 84 | 2.7 | | 286 |
| 1 | Leaf | Enzym. | | | | | 0.038 | 501 |
| 1 | –, mature | Enzym. | | | | 25.6 | | 287 |
| 1 | –, senescent | Enzym. | | | | 7.8 | | 287 |
| 1 | Shoot | Enzym. | 7.36 | 34.1 | 10.5 | | 0.0357 | 288 |
| 1 | Root | Enzym. | | 43.3 | | | 0.0114 | 288 |
| *Oryza sativa* L. (Rice) | | | | | | | | |
| 1 | Grain[a] | Enzym. | 61 | 1800 | 360 | 130 | | 289 |
| 1 | Seed, milky stage | PC/PC | + | | | | | 512 |
| 1 | Leaf[a,b] | Enzym. | | | | | 0.100 | 513 |
| 1 | Seedling[a,f] | Enzym. | | | | | 10 | 514 |
| *Persea americana* Mill. (Avocado) | | | | | | | | |
| 1 | Fruit | $^{31}$P NMR | | + | | | | 515 |
| 1 | Fruit | Enzym. | | | | | 0.34 | 516 |
| 1 | –, mesocarp[h] | Enzym. | | 9 | 3 | 29 | | 290 |
| *Persea gratissima* Gaertn. f. (Avocado) | | | | | | | | |
| 1 | Leaf | PC/PC | | + | | | | 517 |
| *Phaseolus coccineus* L. (Scarlet Runner Bean) | | | | | | | | |
| 1 | Seedling, cotyledon | Enzym. | | | | | 0.9 | 518 |
| 1 | –, leaf | Enzym. | | | | | 0.60 | 518 |
| 1 | –, root | Enzym. | | | | | 0.09 | 518 |
| 1 | –, stem | Enzym. | | | | | 0.10 | 518 |
| *Phaseolus vulgaris* L. (Beans) | | | | | | | | |
| 1 | Leaf[a] | PC/PE | | 29.7[o] | 15.5 | | | 38 |
| 1 | Leaf[a] | Enzym. | | 210 | 110 | 100 | | 291 |
| 1 | Leaf[h] | Enzym. | 0.87 | 2.86 | | | | 519 |

*nmol/g fresh weight basis unless stated otherwise; [a]Basis unstated; [b]nmol/mg chlorophyll; [c]Almost unmeasurable; [d]nmol/plant part; [e]nmol/axis; [f]nmol/mg protein; [g]μmol/m$^2$; [h]nmol/mL; [i]Dry weight basis; [j]mg C/dm$^2$; [k]mol/mol CABP binding site; [l]μmol/g; [m]μg/g; [n]μg/mm$^2$; [o]Incl. G1P; [p]μmol/mg protein; [q]Conc., m*M*.

*Continued*

**Table 1-8** Glucose and Fructose Phosphates in Plants*—cont'd

| No. | Plant part | Method | G1P | G6P | G1,6P | 6-PG | F1P | F6P | F1,6P | F2,6P | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Leaf | IEC | 1430 | 490 | | | | 430 | 480 | | 22 |
| 1 | Fruit | IEC | | 110 | | | | | | | 520 |
| 1 | Seed[a,d] | Enzym. | | | | | | | | 16 | 521 |
| 1 | Seed, cotyledon | $^{31}$P NMR | | + | | | | + | | | 49 |
| *Picea abies* (L.) Karst. (Norway Spruce) | | | | | | | | | | | |
| 1 | Needle (leaf) | Enzym. | | | | | | 480 | | 1.4 | 293 |
| 1 | Needle (leaf) | Enzym. | Variation in F2,6P level from base to tip | | | | | | | | 522 |
| 1 | Seedling endosperm[a,d] | Enzym. | | 2.6 | | | | | | | 523 |
| 1 | –, embryo[a,d] | Enzym. | | 3.7 | | | | | | | 523 |
| 1 | Root | Enzym. | Variation in F2,6P level from base to tip | | | | | | | | 522 |
| *Pinus silvestris* L. (Scotch Pine) | | | | | | | | | | | |
| 1 | Seedling endosperm[a,d] | Enzym. | | 3.1 | | | | | | | 523 |
| 1 | –, embryo[a,d] | Enzym. | | 1.5 | | | | | | | 523 |
| *Pisum sativum* L. (Peas) | | | | | | | | | | | |
| 1 | Leaf | Enzym. | | 120 | | | | 17 | | | 524 |
| 1 | Leaf[b] | Enzym. | | | | | | | 75.2 | 0.078 | 249 |
| 1 | –, chloroplast | HPLC | | | | | | | + | | 106 |
| 1 | Root[a,l] | Enzym. | | 97 | | | | | | | 294 |
| 1 | Root[f] | Enzym. | | | | | | | | 0.053 | 525 |
| 1 | Root tip | $^{31}$P NMR | | + | | | | | | | 526 |
| 1 | Pea | IEC | + | 527 | | | | 93 | | | 24 |
| 1 | Seed | Enzym. | | 8.0 | | | | 14.5 | 8.0 | | 296 |
| 2 | –, embryo (round) | Enzym. | 31 | 442 | | | | 92 | 26 | 1.415 | 295 |
| | –, embryo (wrinkled) | | 70 | 1253 | | | | 283 | 54 | 0.290 | |
| 1 | –, cotyledon | Enzym. | 35 | 479 | | | | 120 | | | 527 |
| *Populus deltoides* Bartr. ex Marsh (Eastern Cottonwood) | | | | | | | | | | | |
| 1 | Leaf[b] | Enzym. | 24 | 140 | | | | 45 | 25 | 0.030 | 297 |
| *Populus gelrica* (Hioutz.) Houtz. | | | | | | | | | | | |
| 1 | Twig bark[i] | Enzym. | 20 | 400 | | | | 80 | | | 509 |
| 1 | –, xylem[i] | Enzym. | 20 | 300 | | | | 60 | | | 509 |
| 1 | Bark[a,d] | Enzym. | 0.01 | 0.20 | | 0.02 | | 0.04 | 0.004 | | 298 |
| *Populus nigra* L. (Black Poplar) | | | | | | | | | | | |
| 1 | Bark[a,d] | Enzym. | 0.02 | 0.33 | | 0.02 | | 0.06 | 0.004 | | 298 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Populus tremula* L. (European Aspen) | | | | | | | | | |
| 1 | Leaf[e] | PC/PE | | 83.4[o] | | 34.8 | | | 38 |
| *Prunus armeniaca* L. (Apricot) | | | | | | | | | |
| 1 | Leaf[a] | PC/PE | | 26.6 | | 7.7 | | | 37 |
| *Pyrus communis* L. (Pear) | | | | | | | | | |
| 1 | Fruit | Enzym. | | + | | 8.0 | 3.5 | 0.006 | 299 |
| 1 | –, skin | IEC | | | | | + | | 19 |
| *Quercus rubra* L. (Red Oak) | | | | | | | | | |
| 1 | Leaf[g] | Enzym. | Data not given | | | | | | 282 |
| *Raphanus sativus* L. (Radish) | | | | | | | | | |
| 1 | Leaf | Enzym. | | 68 | | 32 | 27 | | 300 |
| *Rhododendron ponticum* L. (Common Rhododendron) | | | | | | | | | |
| 1 | Detached leaf | Enzym. | | 78 | 5 | 16 | 0.8 | | 301 |
| *Ricinus communis* L. (Castor Bean) | | | | | | | | | |
| 1 | Seed, endosperm[a,d] | Enzym. | | 0.176 | | 0.074 | 0.015 | | 302 |
| 1 | –, endosperm[a,b] | Enzym. | | | | | | 0.169 | 528 |
| 1 | Seedling, cotyledon | Enzym. | 151 | 2000 | | 600 | 6.7 | 0.55 | 303 |
| 1 | –, hypocotyl | Enzym. | 9 | 395 | | 64 | 3 | | 304 |
| 1 | –, phloem exudate[h] | Enzym. | 80 | 550 | | 171 | 9 | | 304 |
| *Saccharum* spp., hybrid | | | | | | | | | |
| 1 | Internode[a,d] | Enzym. | | | | | F2,6P | 0.157<br>-0.936 | 529 |
| *Saccharum officinarum* L. (Sugar Cane) | | | | | | | | | |
| 1 | Leaf | PC/PC | + | + | | + | | | 306 |
| 1 | Root | PC/PC | + | + | | + | | | 306 |
| 1 | Stalk, third internode[p] | Enzym. | | 13.0<br>and variation from third to ninth internode | | 7.9 | 1.8 | 0.4 | 307 |
| *Saccharum officinarum* × *S. spontaneum* × *S. barberi* | | | | | | | | | |
| 1 | Leaf[g] | Enzym. | 12 | 74 | | 36 | 43 | | 530 |
| *Salix triandra* L. (Almond Willow) | | | | | | | | | |
| 1 | Phloem exudate | TLC/TLC | | + | + | + | + | | 309 |
| *Secale cereale* L. (Rye) | | | | | | | | | |
| 1 | Root tip[q] | Enzym. | | 0.078 | | | | | 531 |
| 1 | Leaf chloroplast (diploid)[m] | Enzym. | 64.4 | 37.9 | | 65.1 | | | 391 |
| 1 | Leaf chloroplast (tetraploid)[m] | Enzym. | 67.3 | 116.3 | | 44.5 | | | 391 |
| *Sesamum alatum* Thonn. | | | | | | | | | |
| 1 | Leaf[b] | Enzym. | | | | 22.6 | 83.8 | | 310 |
| *Sesamum indicum* L. (Sesame) | | | | | | | | | |
| 1 | Leaf[b] | Enzym. | | | | 18.9 | 52.5 | | 310 |

*nmol/g fresh weight basis unless stated otherwise; [a]Basis unstated; [b]nmol/mg chlorophyll; [c]Almost unmeasurable; [d]nmol/plant part; [e]nmol/axis; [f]nmol/mg protein; [g]μmol/m$^2$; [h]nmol/mL; [i]Dry weight basis; [j]mg C/dm$^2$; [k]mol/mol CABP binding site; [l]μmol/g; [m]μg/g; [n]μg/mm$^2$; [o]Incl. G1P; [p]μmol/mg protein; [q]Conc., m*M*.

*Continued*

**Table 1-8** Glucose and Fructose Phosphates in Plants*—cont'd

| No. | Plant part | Method | G1P | G6P | G1,6P | 6-PG | F1P | F6P | F1,6P | F2,6P | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Solanum tuberosum* L. (Potato) | | | | | | | | | | | |
| 1 | Tuber[i,k] | LePage | 0 | 3.50 | | | | 0.17 | 0 | | 13 |
| 1 | Tuber | IEC | 114 | 722 | | | | 306 | 48 | | 316 |
| 1 | Tuber | PC/PC | + | + | | | | + | + | | 9 |
| 1 | Tuber[a] | PC/PC | 18 | 60 | | 3 | | 22 | 1.0 | | 314 |
| 14 | Tuber | PC/PC | tr | + | | | | + | | | 313 |
| 1 | Tuber | PC | | | | | + | + | + | | 315 |
| 1 | Tuber | PE | + | | | | + | + | | | 39 |
| 1 | Tuber | Enzym. | 11 | 110 | | | | | | | 318 |
| 1 | Tuber | Enzym. | | | | | | 28 | 1.5 | 0.03 | 317 |
| 3 | Tuber | Enzym. | | | | | | | | 0.2-0.7 | 532 |
| | | and variation in G1P, G6P, F6P, F1,6P and F2,6P levels along the stolon-apex axis | | | | | | | | | 533 |
| 1 | Mature tuber | Enzym. | | 115 | | | | 20 | 0.3 | | 258 |
| 1 | Developing tuber | HPLC | 15.7 | 157.5 | | | | 68.5 | | | 473 |
| 1 | –, starch grain[m] | Enzym. | | 15 | | | | | | | 318 |
| 1 | Leaf | Enzym. | | | | | | | | 0.061 | 501 |
| 1 | Leaf | Enzym. | | 208 | | | | 42 | | | 311 |
| 1 | –, stroma[b] | Enzym. | | 24 | | | | 23 | 35 | | 312 |
| 1 | –, cytosol[b] | Enzym. | | 85 | | | | 59 | 3 | | 312 |
| *Sorghum bicolor* (L.) Moench (Sorghum) | | | | | | | | | | | |
| 1 | Leaf[b] | Enzym. | | | | | | | | 0.1 | 320 |
| 1 | Root tip | $^{31}$P NMR | | + | | | | | | | 44 |
| *Spinacia oleracea* L. (Spinach) | | | | | | | | | | | |
| 1 | Root[a,l] | Enzym. | | 188 | | | | | | | 294 |
| 1 | Leaf | PC/PC | | + | + | | | + | + | | 321 |
| 1 | Leaf | $^{31}$P NMR | | 7.0 | | + | | | | | 50 |
| 1 | Leaf[a,b] | Enzym. | 16.8 | 87.9 | | | | | | | 393 |
| 1 | Leaf[b] | Enzym. | 20 | 280 | | | | 90 | 10 | 0.075 | 322 |
| 1 | Leaf[a,b] | Enzym. | | | | | | 83 | 6 | 0.095 | 269 |
| 1 | Leaf | Enzym. | | | 1.4 | | | | | | 396 |
| 1 | –, stroma[a,b] | Enzym. | | 48 | | | | 34 | 35 | | 325 |
| 1 | –, cytosol[a,b] | Enzym. | | 82 | | | | 27 | 2.3 | | 325 |
| 1 | –, cytosol[a,b] | Enzym. | | | | | | | | 0.222 | 534 |
| 1 | Leaf, protoplast[b] | Enzym. | | 81.2 | | | | 29.7 | 36.9 | | 326 |
| 1 | –, chloroplast[b] | Enzym. | | 35.9 | | | | 16.1 | 30.7 | | 326 |
| 1 | –, chloroplast[d] | Enzym. | | | | | | | | 0 | 534 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, extrachloroplast[b] | Enzym. | | 61.0 | | | 17.9 | 2.8 | | 326 |
| 1 | –, chloroplast[a,b] | IEC | | | | | | 2.20 | | 20 |
| *Spirodela oligorrhiza* (Kurz.) Hegelm. (Duckweed) | | | | | | | | | | |
| 1 | Whole plant | PC/PC | 50 | 500 | | 18 | 100 | 40 | | 327 |
| *Tilia platyphyllos* Scop. (Large-Leaved Linden) | | | | | | | | | | |
| 1 | Phloem exudate | TLC/TLC | | + | | + | + | | | 328 |
| *Trifolium pratense* L. (Red Clover) | | | | | | | | | | |
| 1 | Stem[l] | Enzym. | | 0.64 | | | | | | 535 |
| 1 | Leaf[n] | HPLC | | | | 6.1 | | | | 474 |
| *Trifolium repens* L. (White Clover) | | | | | | | | | | |
| 1 | Creeping stem[l] | Enzym. | | 0.41 | | | | | | 535 |
| *Trifolium subterraneum* L. (Sub Clover) | | | | | | | | | | |
| 1 | Whole plant | IEC | | 1930 | | | 310 | | | 329 |
| *Triticosecale* Witt. (Triticale) | | | | | | | | | | |
| 1 | Leaf[b] | Enzym. | | | | | | | 0.070 | 536 |
| *Triticum aestivum* L. (Wheat) | | | | | | | | | | |
| 1 | Grain[a,d] | Enzym. | 1.7 | 34.0 | | | 5.0 | 4.0 | 0.108 | 537 |
| 1 | –, endosperm | Enzym. | 10.8 | 224 | 4.9 | | 54.1 | | | 538 |
| 1 | Root[a,l] | Enzym. | | 179 | | | | | | 294 |
| 1 | –, tip[q] | Enzym. | | 0.108 | | | | | | 531 |
| 1 | 6-day root[i] | Enzym. | | | | | | 0.42 | | 330 |
| 1 | Leaf[a,b] | Enzym. | 26 | 115 | | | 77 | 11 | 0.191 | 323 |
| 1 | Leaf[i,m] | Enzym. | | 106.6 | | 99.5 | | | | 539 |
| 1 | Seedling, leaf | PC/PE | + | | | | + | | | 331 |
| 1 | Shoot[i] | Enzym. | | | | | | 2.3 | | 330 |
| *Urtica dioica* L. (Stinging Nettle) | | | | | | | | | | |
| 1 | Leaf | Enzym. | | | | | | | 0.652 | 501 |
| *Vicia faba* L. (Broad Bean) | | | | | | | | | | |
| 1 | Leaf | PC/PC | | + | + | | + | + | | 321 |
| *Vigna mungo* (L.) Hepper (Black Gram) | | | | | | | | | | |
| 1 | Seedling, cotyledon[a,d] | Enzym. | | 8.8 | | 0.5 | 1.5 | | | 540 |
| 1 | –, embryonic axis[a,d] | Enzym. | | 30.1 | | 0.6 | 6.0 | | | 540 |
| 1 | –, hypocotyl tip | Enzym. | | 43.1 | | 0.2 | 10.9 | 1.3 | 0.186 | 332 |
| | | and variation in F2,6P content from base to tip | | | | | | | | 541 |
| 1 | Root tip | $^{31}$P NMR | | + | | | | | | 542,543 |
| *Vigna radiata* (L.) R. Wilcz. (Mung Bean) | | | | | | | | | | |
| 1 | Seedling | Enzym. | | 58 | 12 | | 22 | 44 | 21 | 262 |

*nmol/g fresh weight basis unless stated otherwise; [a]Basis unstated; [b]nmol/mg chlorophyll; [c]Almost unmeasurable; [d]nmol/plant part; [e]nmol/axis; [f]nmol/mg protein; [g]µmol/m$^2$; [h]nmol/mL; [i]Dry weight basis; [j]mg C/dm$^2$; [k]mol/mol CABP binding site; [l]µmol/g; [m]µg/g; [n]µg/mm$^2$; [o]Incl. G1P; [p]µmol/mg protein; [q]Conc., m*M*.

*Continued*

**Table 1-8** Glucose and Fructose Phosphates in Plants*—cont'd

| No. | Plant part | Method | G1P | G6P | G1,6P | 6-PG | F1P | F6P | F1,6P | F2,6P | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Leaf[b] | Enzym. | | | | | | | 70.3 | 0.080 | 249 |
| *Vitis vinifera* (Wine Grape) | | | | | | | | | | | |
| 1 | Seedless berry | Enzym. | | 117 | | | | 30 | 0.14 | | 333 |
| 1 | Juice | | | | | | | 0 | | | 334 |
| *Xanthium strumarium* L. (Cocklebur) | | | | | | | | | | | |
| 1 | Leaf[a,b] | Enzym. | | | | | | | 33 | | 336 |
| *Yucca flaccida* Haw. (Weak-Leaf Yucca) | | | | | | | | | | | |
| 1 | Phloem exudate | TLC/TLC | | + | | | + | + | + | | 309 |
| *Zea mays* L. (Corn) | | | | | | | | | | | |
| 1 | Root | PC/PC | 313 | 456 | | | | | | | 12 |
| 1 | Root | TLC/TLC | + | + | | | + | + | | | 12 |
| 1 | Root tip | $^{31}$P NMR | | + | | | | | | | 42,43,544 |
| 1 | Leaf[b] | PC/PC | | 110 | | | | 61 | 21.4 | | 337 |
| 1 | Leaf[a,b] | Enzym. | | 105 | | | | 58 | 21 | 0.13 | 545 |
| 1 | –, midrib[b] | Enzym. | | 287 | | | | 135 | 78 | | 340 |
| 1 | –, lamina[b] | Enzym. | | 121 | | | | 58 | 46 | | 340 |
| 1 | Grain, endosperm[i] | Enzym. | 0.7 | 38.1 | | | | 5.9 | 2.7 | | 342 |
| 1 | –, endosperm | Enzym. | 140.5 | 2180.0 | | | | 558.9 | 467.2 | 6.1 | 546 |
| 1 | –, starch granule[i] | Enzym. | 0.2 | 8.6 | | | | 1.8 | 0.5 | | 342 |
| 1 | Flower, ovary | Enzym. | 0.13 | 2.2 | | | | 0.18 | | | 343 |

*nmol/g fresh weight basis unless stated otherwise.
[a]Basis unstated.
[b]nmol/mg chlorophyll.
[c]Almost unmeasurable.
[d]nmol/plant part.
[e]nmol/axis.
[f]nmol/mg protein.
[g]µmol/m$^2$.
[h]nmol/mL.
[i]Dry weight basis.
[j]mg C/dm$^2$.
[k]mol/mol CABP binding site.
[l]µmol/g.
[m]µg/g.
[n]µg/mm$^2$.
[o]Incl. G1P.
[p]µmol/mg protein.
[q]Conc., m*M*.

*Into a 1.0-cm absorption cell are pipetted 0.65 ml of water, 0.15 ml of 0.25*M *glycylglycine buffer, pH 7.5, 0.10 ml of 0.1*M *$MgCl_2$, 0.10 ml of triphosphopyridine nucleotide (TPN) (1.4 μ*M*/ml), and 0.02 ml of glucose-6-phosphate dehydrogenase (ca 0.02 mg). The solution is mixed, and an initial density reading at 340 mm is taken. The glucose-6-phosphate sample . . . is added, and the increase in density at 340 mm is followed until a constant value is reached. The amount of glucose-6-phosphate added is calculated from the relation G6P (micromoles)* $= (d_f - d_o) \times 1.04/6.22$ *where $d_f$ and $d_o$ are the final and initial density readings, respectively.*

Horecker, B. L.; Wood, W. A., "D-Glucose-6-Phosphate", *Methods Enzymol.* **1957**, *3*, 152–154,[547] reprinted by permission of Elsevier, © 1957.

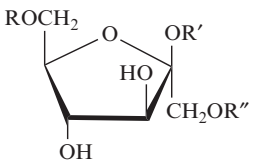
Metabolites that are converted to G6P upon treatment with the appropriate enzyme, such as G1P/PG mutase or F6P/PG isomerase, can be assayed by the same method. Others are ATP/hexokinase,[282] UDPG/UDPG pyrophosphorylase,[527] and ADPG/ADPG pyrophosphorylase.[548] Kumar and Singh[548] were able to determine all six metabolites in a wheat extract by adding two units (5 mL) of each enzyme in sequence to the assay mixture (1.5 mL) in a cuvette and recording the absorbance after each addition. G1P and G6P may also be determined by conversion to F6P with PG mutase and PG isomerase and assayed for F6P by the luciferin-luciferase method (Fig. 1-5, steps 2 and 3).[481]

Two enzymatic methods have been reported for the determination of G1,6P in plant extracts, both of which require brief heating with dilute alkali to remove interfering substances. In one, G1,6P is hydrolyzed with 0.1*N* HCl for 7 min at 100 °C and assayed for G6P by fluorimetry.[488] In the other, G1,6P is assayed as a cofactor of the PG mutase reaction (Fig. 1-5, step 2) using G1P and dephosphorylated PG mutase to convert the G1,6P to G6P.[396]

6-PG may be determined by enzymatic oxidation to Ru5P and $CO_2$ by NADP in the presence of 6-PG dehydrogenase (Table 1-3, reaction 7). The amount of 6-PG is calculated from the change in absorbance at 340 nm.[257]

## Fructose Phosphates

This group comprises two monophosphates (F1P and F6P) and two bisphosphates (F1,6P and F2,6P).




**F1P**, R = R′ = H, R″ = $P(O)(OH)_2$
**F6P**, R = $P(O)(OH)_2$, R′ = R″ = H
**F1,6P**, R = R″ = $P(O)(OH)_2$, R′ = H
**F2,6P**, R = R′ = $P(O)(OH)_2$, R″ - H

D-Fructose 1-Phosphate (F1P), $C_6H_{13}O_9P$; Beilstein **1**, $E^{IV}$ 4421. *β-D-Fructofuranose 1-(Dihydrogen Phosphate)* [1956].

D-Fructose 6-Phosphate (F6P), $C_6H_{13}O_9P$; Beilstein **1**, $E^I$ 464, $E^{IV}$ 4423; **31**, 337. Neuberg ester, *β-D-Fructofuranose 6-(Dihydrogen Phosphate)* [1943].

D-Fructose 1,6-Bisphosphate (F1,6P), $C_6H_{14}O_{12}P_2$; Beilstein **1**, $E^I$ 464, $E^{IV}$ 4424; **31**, 337. Harden-Young ester, *β-D-Fructofuranose 1,6-Bis(dihydrogen Phosphate)* [1952].

D-Fructose 2,6-Bisphosphate (F2,6P), $C_6H_{14}O_{12}P_2$; not listed in Beilstein. *β-D-Fructofuranose 2,6-Bis(dihydrogen Phosphate)* [1981].

## Occurrence

F6P and F1,6P are metabolites of the photosynthetic carbon reduction cycle (Calvin cycle) of higher plants (Fig. 1-5). In step 6, DHAP undergoes an aldol condensation with G3P forming F1,6P. In step 7, F1,6P is hydrolyzed by a specific fructose 1,6-bisphosphatase to F6P. In step 8, F6P reacts with another molecule of G3P, forming E4P and Xu5P. These reactions all take place within the chloroplast, found only in the green leaf.

F6P and F1,6P are also metabolites of the Embden-Meyerhof-Parnas glycolysis pathway, a sequence common to all of the higher plants. F6P, derived from fructose by phosphorylation with ATP (step 15) or from G6P by the action of G6P isomerase (step 3), is phosphorylated to F1,6P by ATP (step 4). The F1,6P is then split into G3P and DHAP by aldolase (step 5). These reactions take place in the cytoplasm outside any organelle.

In addition, F6P is a metabolite of the pentose phosphate respiratory pathway (hexose monophosphate shunt). F6P, derived from E4P and Xu5P by the action of transketolase (step 9) or from G3P and Se7P by the action of transaldolase (step 10), is converted to its isomer G6P by G6P isomerase (step 11). These reactions take place in the cytoplasm and (during periods of darkness) in chloroplasts.

F2,6P is a recently discovered metabolite whose function in the higher plants is to regulate the synthesis of sucrose by controlling the enzymes that catalyze the F6P↔F1,6P interconversion. It is formed from F6P by phosphorylation with ATP (step 16) and is hydrolyzed back to F6P by a specific phosphatase (step 17). As a signal regulator, its content in plant tissue, usually at the nanomole level, can change dramatically in response to changes in metabolite level, nitrogen or phosphorus level, light level, and other factors.

The presence of F1P in potato,[39] carrot,[486] turnip,[486] and artichoke[500] tubers has been established by experiments with [$^{32}$P]-$KH_2PO_4$ and [$^{14}$C]-fructose, but its source could not be determined and it did not appear to be metabolized.[500] F1P was postulated to be a metabolite in the photosynthesis of sucrose in cotton[263] and sugar beet[483] leaves, but this was later retracted.[549]

## Physical Properties

Fructose 1-Phosphate

F1P [R.N. 15978-08-2; see also 52050-05-2]: $[\alpha]_D^{20}$ −52.5°.[550] Spectra: UV,[102] IR (fig.),[94] CD,[102] GC/MS,[96] $^{13}$C NMR,[551] $^{31}$P NMR.[68] Chromatography: PC,[9] TLC,[160] IEC,[552] GC.[446] Electrophoresis: PE,[9] zone,[88] isotachophoresis.[88]
$BaC_6H_{11}O_9P{\cdot}2H_2O$ [R.N. 53823-70-4]: Amorphous solid,[550] $[\alpha]_D^{26}$ −30.4° ($H_2O$).[553]
$(C_6H_{11}NH_2)_2C_6H_{13}O_9P$ [R.N. 74381-67-2]: Fine long rods, sol. methanol, insol. ethyl acetate.[553]
$(C_{23}H_{26}N_2O_4)_2C_6H_{13}O_9P$ (brucine salt): $[\alpha]_{546}^{20}$ − 52.1°($H_2O$).[554]

Fructose 6-Phosphate

F6P [R.N. 643-13-0; see also 41452-29-3]: $[\alpha]_D^{21}$ +2.5°,[555] p$K_a$ 0.97[555] and 6.35[130]; redox potential,[427] countercurrent distribution.[141] Spectra: UV,[102] IR (fig.),[94] CD,[102] GC/MS,[96] $^1$H NMR,[131] $^{13}$C NMR (fig.),[551] $^{31}$P NMR,[68] ESR.[406] Chromatography: PC,[9,32] TLC,[36] IEC,[86,134] HPTLC,[407] GC,[408] HPLC,[26] IC (fig.).[107] Electrophoresis: PE,[32] TLE,[36] zone,[88] CZE,[89] CE,[90] isotachophoresis.[88]
$Na_2C_6H_{11}O_9P{\cdot}2H_2O$ [R.N. 26177-86-6]: White, amorphous powder. Spectra: $^1$H, $^{23}$Na, and $^{31}$P NMR.[556] Heptahydrate: Orthorhombic cryst., d 1.61; X-ray.[557]
$K_2C_6H_{11}O_9P{\cdot}6H_2O$ [R.N. 99481-18-2]: Monoclinic cryst., d 1.66; X-ray.[558]
$BaC_6H_{11}O_9P$ [R.N. 6035-54-7]: White powder, $[\alpha]_D^{19}$ +3.58° ($H_2O$).[559]

Fructose 1,6-Bisphosphate

F1,6P [R.N. 488-69-7; see also 34693-15-7]: $[\alpha]_D^{17}$ +4.04° (2*N* HBr),[559] p$K_a$ 1.48,[560] 6.425 and 7.276[561]; redox potential,[427] countercurrent distribution.[141] Spectra: UV (fig.),[561] IR (fig.),[103] FTIR (fig.),[95] Raman,[562] CD,[102] ORD (fig.),[561] GC/MS,[96] $^1$H NMR (fig.),[103,131] $^{13}$C NMR (fig.),[103] $^{31}$P NMR (fig.),[103] ESR.[406] Chromatography: PC,[9,32] TLC,[160] IEC,[86,134] HPTLC,[407] GC,[408] HPLC,[26] HPLC-MS-MS,[100] IC (fig.).[107] Electrophoresis: PE,[32] TLE,[105] zone,[88] CZE,[89] CE,[90] isotachophoresis.[88]
$Na_3C_6H_{11}O_{12}P_2$ [R.N. 38099-82-0]: mp 125 °C, $[\alpha]_D$ +2.6° ($H_2O$).[563] Octahydrate [R.N. 81028-91-3]: Monoclinic cryst., d 1.704; X-ray.[564]
$Na_4C_6H_{10}O_{12}P_2$ [R.N. 23784-19-2]: Hygroscopic, yellowish powder, $[\alpha]_D^{21}$ +2.79° ($H_2O$).[565]
$Mg_2C_6H_{10}O_{12}P_2$: Colorless granules; water solubility, 30%.[566]
$Ca_2C_6H_{10}O_{12}P_2$ [R.N. 6055-82-9]: Amorphous solid[567]; heat of combustion 2808 kJ/mol.[126]
$BaC_6H_{12}O_{12}P_2$: Snow-white solid, very sol. $H_2O$ (∼1:2).[559]
$Ba_2C_6H_{10}O_{12}P_2$ [R.N. 6035-52-5]: Fluffy, snow-white powder, sparingly sol. $H_2O$.[559]
$(C_6H_{11}NH_2)_3C_6H_{14}O_{12}P_2{\cdot}H_2O$: Rods, mp 163-166 °C dec.[568]

Fructose 2,6-Bisphosphate

F2,6P [R.N. 77164-51-3; see also 79082-92-1]: Conformation.[569] Spectra: $^1$H NMR (fig.), $^{13}$C NMR (fig.), $^{31}$P NMR (fig.).[569] Chromatography: PC,[570] IEC,[570] HPLC.[428] Electrophoresis: CZE.[89]
$C_6H_{11}NH_2$ salt: Powder.[570]

## Synthesis

F1P may be prepared (a) by phosphorylation of 2,3,4,5-diisopropylidene-D-fructopyranose with $POCl_3$,[571] $P_2O_5$,[553] or diphenyl phosphorochloridate,[572] (b) by partial enzymatic hydrolysis of F1,6P with bone phosphatase,[554] or (c) by aldolase-catalyzed condensation of DHAP with D-glyceraldehyde.[554] F6P may be prepared (a) by partial hydrolysis of F1,6P with HCl at 35 °C[559] or liver hexose diphosphatase at pH 9.7[573] or (b) by phosphorylation of D-fructose with hexokinase.[101] F1,6P may be prepared (a) by phosphorylation of sucrose with baker's yeast[574] or (b) by aldolase-catalyzed condensation of DHAP with G3P.[101] F2,6P may be prepared (a) from $F_6P$ by phosphorylation with phosphoric acid[575] or (b) from F1,6P by DCC-promoted cyclization followed by alkaline hydrolysis.[576]

## Hydrolysis

The rate of hydrolysis of F1P in 1*N* HCl at 100 °C is $2.68 \times 10^{-3}$ $s^{-1}$.[554]

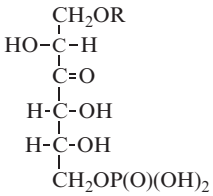
Hydrolysis of F6P in 1*N* HCl at 100 °C liberates orthophosphate quantitatively ($k = 1.67 \times 10^{-4}$ $s^{-1}$),[577] but in 0.75*M* NaOH only 80% of the orthophosphate is liberated owing to degradation of the sugar moiety.[578] For the behavior of F6P over the pH range 0-8.3 at 100 °C, see Fleury *et al.*[579] The hydrolysis is catalyzed by molybdate (fivefold at pH 5.8),[204] Th(IV),[215] Ce(III), and other M(III) salts,[216] and by UV radiation.[217] Measurements on the hydrolysis of F6P with alkaline phosphatase gave $\Delta G^\circ$ 13.70 kJ/mol, $\Delta H^\circ$ −7.61 kJ/mol, and $\Delta C^\circ_P$ −28 J/(mol K).[383]

Hydrolysis of F1,6P in 1*N* HCl at 100 °C liberates $P_i$ in two stages ($k = 2.0 \times 10^{-3}$ $s^{-1}$ for $P_1$ and $1.5 \times 10^{-4}$ $s^{-1}$ for $P_6$),[580] but alkaline hydrolysis is complicated by degradation of the sugar moiety to saccharinic acid,[581] lactic acid,[565] and pyrotartaric acid.[578] The hydrolysis is catalyzed by molybdate,[204] Th(IV),[215] Ce(III), and other M(III) salts,[216] and by UV radiation.[217]

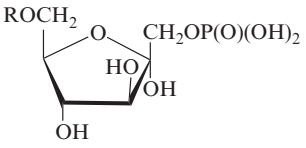
Hydrolysis of F2,6P with 0.5*N* HCl at 30 °C for 15 min liberates equimolar amounts of F6P and inorganic phosphate.[570] Its half-life at pH 4 is 5.2 min.[576] F2,6P is stable to base, no change being noted after 30 min in 0.01*M* NaOH at 100 °C.[576]

## Structure

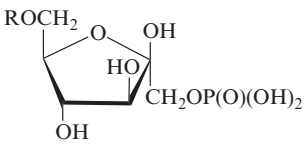
F1P shows no free keto form (<1.0%) in aqueous solution.[94] F6P solutions show 2.5%[94] to 4.1%[582] of the open-chain keto form **12** and 20% of the α-furanose anomer **13**.[583] The rate of ring-opening at pH 7.5 and 40 °C is 18 $s^{-1}$ for the α anomer **13** and 21 $s^{-1}$ for the β anomer **14**.[348]




**12**, R = H
**15**, R = $P(O)(OH)_2$




**13**, R = H
**16**, R = $P(O)(OH)_2$




**14**, R = H
**17**, R = $P(O)(OH)_2$

The behavior of F1,6P is analogous: Aqueous solutions show 1.7%[103] to 2.0%[582] of open-chain keto form **15** (not hydrated to an appreciable extent [<0.1%] to the *gem*-diol[103]) and 10% of the α-furanose anomer **16**.[104] The rates of ring-opening at pH 7.2 and 25 °C are about 8 $s^{-1}$ for the α anomer **16** and 35 $s^{-1}$ for the β anomer **17**.[582]

## Separation and Analysis

### *(1) LePage and Umbreit Method*[3]

F6P and F1,6P are present in different fractions of the TCA extract, together with other phosphate esters (see p 2). They are determined by analysis for fructose, on the assumption that no other fructose-containing compounds are present. This method has been superseded by those which follow.

### *(2) Chromatographic Methods*

F6P and F1,6P in plant extracts can be separated from other phosphate esters and from each other by IEC, by HPLC, or by two-dimensional PC, TLC, PC/PE, or TLC/TLE (Table 1-8). Quantitative data have been reported in several instances. F1P has been detected in a few plant extracts by two-dimensional PC, but F2,6P occurs at too low a level to be detected by any chromatographic method.

## Analysis Without Separation

### *(1) $^{31}$P NMR Method*

F6P and F1,6P have been identified in a few plant extracts by high-field FT $^{31}$P NMR (Table 1-8). F6P was also tentatively identified in the spectra of sycamore cells suspended in a $P_i$-free culture medium.[46]

### *(2) Enzymatic Methods*

F1P may be determined by an indirect enzymatic method coupled to the reduction of DHAP to α-GP by NADH (Table 1-3, reaction 2) using aldolase to convert the F1P to DHAP.[486] F6P is usually determined by an indirect enzymatic method coupled to the oxidation of G6P by NADP (Table 1-3, reaction 6 and Fig. 1-5, steps 11 and 12):

> *Glc-6-P concentration was measured in 1 mL of assay mixture containing 0.2*M *triethanolamine/HCl, pH 7.6, 5 m*M *$MgCl_2$, 0.5 m*M *$NADP^+$, 0.5 unit glucose 6-phosphate dehydrogenase (EC 1.1.1.49) and 25 μL of plant extract. After total oxidation of Glc-6-P, Fru-6-P concentration was determined by addition of 1 unit hexose-phosphate isomerase (EC 5.3.1.9).*
>
> Sola, M. M.; Gutiérrez, M.; Vargas, A. M., "Regulation of Hexose-Phosphate Cycle Determines Glucose and Fructose Accumulation in Cherimoya (*Annona cherimola* Mill.) during Ripening", *J. Plant Physiol.* **1994**, *144*(4/5), 569–575,[479] reprinted by permission of Elsevier, © 1994.

F6P may also be determined by enzymatic phosphorylation to F1,6P with PFK kinase/ATP (Fig. 1-5, step 4) and assayed directly by measuring the consumption of ATP by the luciferin/luciferase method[481] or indirectly by the DHAP/NADH route as shown below[242]:

F1,6P may be determined by indirect enzymatic methods coupled to the reduction of DHAP to α-GP (Table 1-3, reaction 2),[242] to the oxidation of G3P to 3-PGA (Table 1-3, reaction 1),[258] or to the oxidation of G6P to 6-PG (Table 1-4, reaction 6).[236]

$$\text{F6P} \xleftarrow{7} \text{F1,6P} \xrightarrow{5} \begin{cases} \text{DHAP} \rightarrow \text{α-GP} \\ \text{G3P} \rightarrow \text{3-PGA} \end{cases}$$

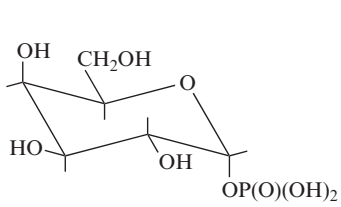
The first two methods employ F1,6P aldolase and triose-P isomerase to convert the F1,6P to DHAP or G3P. The DHAP reduction method, which was used in the majority of the enzymatic analyses reported in Table 1-8, is described on pp 13-14. The G3P oxidation method was employed by Barker *et al.*[258,584] for the fluorimetric analysis of F1,6P in a variety of plant extracts. The third method employs F1,6P phosphatase to convert the F1,6P to F6P and PG isomerase to convert the latter to G6P.[387]

F2,6P is acid-labile and therefore requires a sample that has been extracted from plant tissue at pH 7 or above. Most determinations are made by the procedure of van Schaftlingen *et al.*[585] which is based on the stimulation of the potato enzyme $PP_i$-PFK [E.C. 2.7.1.90] by F2,6P in the phosphorylation of F6P by pyrophosphate ($F6P + PP_i \rightarrow F1,6P + P_i$). The assay then follows the DHAP reduction method for F1,6P described above. An important modification of the original procedure is the use of an acid wash to remove traces of F2,6P from the F6P reagent used in the assay.[586]

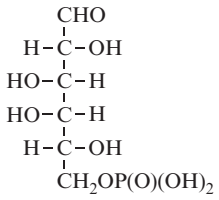
> *The assay medium (1 ml) contained 50 m*M *Tris/HCl, pH 8.0, 5 m*M *$MgCl_2$, 1 m*M *EDTA, 0.1 m*M *DTT, 0.15 m*M *NADH, 1 m*M *acid-washed Fru-6-P, 0.5 unit fructose 1,6-bisphosphate aldolase (E.C. 4.1.2.13), 1.5 unit triose-phosphate isomerase (E.C. 3.3.1.1), 0.5 unit glycerol 3-phosphate dehydrogenase (EC 1.1.1.8), approximately 50 mUnit potato tuber $PP_i$-PFK and 0.1 mL of plant extract. The reactions were initiated with 0.5 m*M *$Na_4PP_i$ (previously adjusted to pH 8.0) after preincubation for 5 min at 30 °C. The assays were carried out for 10 min at 30 °C. Fru-2,6-$P_2$ concentration was calculated with respect to a standard curve. Recovery experiments (Ball and ap Rees, 1988) always gave values greater than 90%.*
>
> Sola, M. M.; Gutiérrez, M.; Vargas, A. M., "Regulation of Hexose-Phosphate Cycle Determines Glucose and Fructose Accumulation in Cherimoya (*Annona cherimola* Mill.) during Ripening", *J. Plant Physiol.* **1994**, *144*(4/5), 569–575,[479] reprinted by permission of Elsevier, © 1994.

F2,6P can also be determined by mild acid hydrolysis, provided that the reducing sugar phosphates (G6P, F6P, etc.) are first destroyed by treatment with alkali or $NaBH_4$.[262] The F6P so produced is then analyzed in the usual manner. This method has found little favor, though it is still used as the reference method for purified standards.[5a]

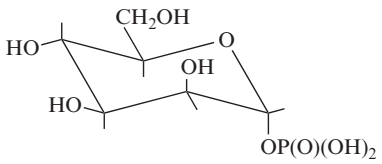
## Galactose and Mannose Phosphates



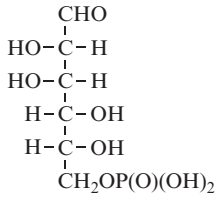

**Gal1P**




**Gal6P**




**Man1P**




**Man6P**

D-Galactose 1-Phosphate (Gal1P), $C_6H_{13}O_9P$; not listed in Beilstein. *α-D-Galactopyranose 1-(Dihydrogen Phosphate)* [1938].

D-Galactose 6-Phosphate (Gal6P), $C_6H_{13}O_9P$; Beilstein **1**, $E_{IV}$ 4383. *D-Galactose 6-(Dihydrogen Phosphate)* [1931].

D-Mannose 1-Phosphate (Man1P), $C_6H_{13}O_9P$; not listed in Beilstein. *α-D-Mannopyranose 1-(Dihydrogen Phosphate)* [1938].

D-Mannose 6-Phosphate (Man6P), $C_6H_{13}O_9P$; Beilstein **1**, $E_{IV}$ 4382. *D-Mannose 6-(Dihydrogen Phosphate)* [1932].

## Occurrence

These phosphates are less well known than those of glucose or fructose. Galactosyl and mannosyl residues are present in plant tissue as components of polysaccharides, glycolipids, or glycoproteins, but both are often toxic when supplied to the plant in the form of free galactose or mannose. Numerous plants have been shown to be capable of metabolizing D-galactose and D-mannose to Gal1P and Man6P, respectively, but few have the enzymes needed to convert these to starch or sucrose. The phosphates accumulate, depleting the supply of cytoplasmic $P_i$.

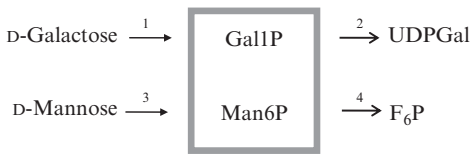



**FIGURE 1-6 Galactose and Mannose Phosphates**. (1) D-Galactokinase [E.C. 2.7.1.6], ATP. (2) UDP-D-galactose pyrophosphorylase [E.C. 2.7.7.10], UTP. (3) Hexokinase [E.C. 2.7.1.1], ATP. (4) Man6P isomerase [E.C. 5.3.1.8].

The known metabolic pathways whereby the plant salvages these sugars are illustrated in Fig. 1-6. In steps 1 and 3, D-galactose and D-mannose (released from their combined forms by enzymatic reactions) are phosphorylated by ATP to Gal1P and Man6P, respectively. The Gal1P reacts with UTP (step 2) to give UDPGal, which is either metabolized to galactosyl polysaccharides, lipids, etc., or isomerized to UDPG, G1P, and ultimately starch.[587] The Man6P is isomerized to F6P (step 4), leading ultimately to sucrose.[588]

Traces of a galactose monophosphate identified as Gal6P have been detected by paper chromatography in duckweed[327] and in the cambial sap of larch.[504] Its source is unknown. The galactose monophosphate formed in the tomato is definitely not the 6-phosphate.[589]

Gal1P and Man6P accumulate in corn (*Zea mays* L.) root and leaf upon treatment with D-galactose and D-mannose, respectively, based upon $^{14}C$ labeling experiments and changes in their high-field FT $^{31}P$ NMR spectra.[587,590] The Man6P is slowly metabolized by a pathway involving Man1P.[590]

## Physical Properties

D-Galactose 1-Phosphate

Gal1P [R.N. 2255-14-3]: $[\alpha]_D^{25}$ +143° ($H_2O$),[591] p$K_a$ 1.00, 6.17,[592] standard transformed Gibbs energy of formation, $\Delta_f G'^{\circ}$.[447] Spectra: GC/MS (fig.),[96] $^1H$ NMR,[593] $^{13}C$ NMR,[594] $^{31}P$ NMR.[68] Chromatography: PC,[29] TLC,[160] IEC,[595] ESI-MS-MS,[403] HPLC-MS-MS.[100] Electrophoresis: PE.[596]

$K_2C_6H_{11}O_9P{\cdot}2H_2O$ [R.N. 19046-60-7]: Crystals, very sol. $H_2O$, insol. EtOH, $[\alpha]_D^{18}$ +108.2° ($H_2O$).[597] Pentahydrate [R.N. 132929-14-7]: Monoclinic crystals, d 1.756. Spectra: X-ray.[598]

$BaC_6H_{11}O_9P{\cdot}3H_2O$ [R.N. 103213-39-4]: Amorphous nonhygroscopic white powder, easily sol. $H_2O$, insol. 50% EtOH, $[\alpha]_D^{25}$ +91° ($H_2O$).[591]

$(Et_3N)_2C_6H_{13}O_9P$ [R.N. 139883-88-8]: $[\alpha]_D^{25}$ +66.5° ($H_2O$).[599]

$(C_6H_{11}NH_2)_2C_6H_{13}O_9P{\cdot}0.5H_2O$ [R.N. 38099-40-0]: Hygroscopic needles, mp 141-143 °C,[600] $[\alpha]_D^{20}$ +78.5° ($H_2O$).[452] Spectra: $^1H$, $^{13}C$, and $^{31}P$ NMR.[422]

D-Galactose 6-Phosphate

Gal6P [R.N. 6665-00-5; see also 33163-99-4]: Colorless glass, $[\alpha]_D^{20}$ +36.5° ($H_2O$).[601] Spectra: GC/MS (fig.),[96] $^{13}C$ NMR,[602] $^{31}P$ NMR.[68] Chromatography: PC,[9,32] GC,[446] IEC,[552] HPLC,[27] IC.[603] Electrophoresis: PE.[32]

$Li_2C_6H_{11}O_9P$ [R.N. 52888-24-1]: $[\alpha]_D^{20}$ +31.6° ($H_2O$).[429]

$BaC_6H_{11}O_9P$ [R.N. 4198-47-4]: $[\alpha]_D^{25}$ +24.5° ($H_2O$).[604]

Brucine salt: Elongated hexagonal plates.[605]

D-Mannose 1-Phosphate

Man1P [R.N. 15978-07-1]: $[\alpha]_D^{25}$ +58° ($H_2O$).[591] Spectra: GC/MS,[96] $^1$H NMR (fig.),[593] $^{13}$C NMR,[606] $^{31}$P NMR.[68] Chromatography: PC,[29] TLC,[160] IEC,[552] HPLC-MS-MS,[100] ESI-MS-MS.[403] Electrophoresis: PE.[596]
$Li_2C_6H_{11}O_9P{\cdot}H_2O$ [R.N. 14985-29-6]: Hygroscopic solid, $[\alpha]_D^{25}$ +46.3° ($H_2O$).[607]
$BaC_6H_{11}O_9P{\cdot}3H_2O$ [R.N. 51306-18-4]: Amorphous nonhygroscopic white powder, easily sol. $H_2O$, insol. 50% EtOH; $[\alpha]_D^{25}$ +36° ($H_2O$).[591]
$(Et_3N)_2C_6H_{13}O_9P$ [R.N. 139883-95-7]: $[\alpha]_D^{25}$ +19.7° ($H_2O$).[599]
$(C_6H_{11}NH_2)_2C_6H_{13}O_9P{\cdot}2H_2O$ [R.N. 51306-17-3]: Colorless cryst., mp 137-138.5 °C, $[\alpha]_D^{20}$ +26° ($H_2O$).[608] Monohydrate: Cryst., mp 181-182 °C.[609]

D-Mannose 6-Phosphate

Man6P [R.N. 3672-15-9]: $[\alpha]_D^{22}$ +13.3° (0.1*N* HCl),[610] $[\alpha]_{546}^{20}$ + 15.1°($H_2O$),[577] p$K_a$ 6.1.[405] Spectra: GC/MS,[96] $^1$H NMR,[611] $^{13}$C NMR,[606] $^{31}$P NMR.[68] Chromatography: PC,[9,32] TLC,[36] IEC,[552] GC,[446] HPLC.[442] Electrophoresis: PE,[32] TLE.[36]
$Li_2C_6H_{11}O_9P$ [52888-25-2]: $[\alpha]_D^{20}$ +7.7° ($H_2O$).[429]
$Na_2C_6H_{11}O_9P$ [R.N. 33068-18-7]: $[\alpha]_D^{25}$ +7.39° ($H_2O$).[611]
$BaC_6H_{11}O_9P{\cdot}2H_2O$: Fine needles, $[\alpha]_D^{20}$ +3.2° ($H_2O$).[429]
$(Et_3N)_2C_6H_{13}O_9P$: $[\alpha]_D$ +10° (MeOH).[612] Spectra: $^1$H NMR.[612]
Brucine salt: Short needles.[577]

## Synthesis

Gal1P may be prepared (a) by phosphorylation of tetra-*O*-acetyl-α-D-galactopyranoside with diphenyl phosphorochloridate[599] or dibenzyl *N*,*N*-diethylphosphoramidite,[451] (b) by phosphorylation of tetra-*O*-acetyl-α-D-galactosyl bromide with $Ag_3PO_4$[597] or silver diphenyl phosphate,[414] (c) by the reaction of penta-*O*-acetyl-β-D-galactopyranoside[452] or MOP β-D-galactopyranoside[422] with anhydrous phosphoric acid, or (d) by enzymatic phosphorylation of D-galactose with galactokinase and ATP in the presence of PEP or acetyl phosphate.[594] Gal6P may be prepared by phosphorylation of D-galactose with polyphosphoric acid,[602] of methyl α-D-galactopyranoside with $POCl_3$,[429] or of di-*O*-isopropylidene-D-galactopyranose with $POCl_3$,[604] diphenyl phosphorochloridate,[601] or bis(2,4-dichlorophenyl)phosphorochloridite.[455]

Man1P may be prepared (a) by phosphorylation of tetra-*O*-acetyl-α-D-mannopyranose with diphenyl phosphorochloridate[599] or dibenzyl *N*,*N*-diethylphosphoramidite,[451] (b) by phosphorylation of tetra-*O*-acetyl-α-D-mannosyl bromide with $Ag_3PO_4$[591] or of the corresponding chloride with silver diphenyl phosphate or silver dibenzyl phosphate,[610] (c) by the reaction of penta-*O*-acetyl-α-D-mannopyranose with anhydrous phosphoric acid,[607] or (d) by reaction of a tri-*O*-acetyl-β-D-mannopyranosyl orthoacetate with dibenzyl phosphate.[609] Man6P may be prepared by phosphorylation (a) of penta-*O*-trimethylsilyl-α-D-mannopyranose[611] or methyl α-D-mannopyranoside[429] with $POCl_3$, (b) of tetra-*O*-acetyl-β-D-mannopyranose with diphenyl phosphorochloridate,[610] (c) of D-mannose with hexokinase and ATP,[613] or (d) by fermentation of mannose with dried yeast.[614]

## Hydrolysis

Gal1P is completely hydrolyzed by 0.09*N* $H_2SO_4$ in 2 min at 100 °C but is unaffected by 0.2*N* NaOH after 30 min at 100 °C.[597] In contrast, Gal6P is only 7% hydrolyzed after 5 h in 0.1*N* $H_2SO_4$ at 100 °C but 90% hydrolyzed in less than 10 min in 0.1*N* NaOH at 100 °C.[615] The hydrolysis of Gal6P is catalyzed by Ce(III) and La(III).[616] Rate constants for the hydrolysis of the four compounds are as follows:

| Compound | Conditions | $k \times 10^{-3}$ min$^{-1}$ | References |
|---|---|---|---|
| Gal1P | 0.25*N* HCl, 25°C | 2.05 | 597 |
| Gal6P | 0.01*N* HCl, 100 °C | 0.87 | 605 |
| Man1P | 0.95*N* $H_2SO_4$, 30 °C | 1.90 | 610 |
| Man6P | 1*N* HCl, 100 °C | 0.67 | 577 |

The α and β anomers of Gal1P and Man1P can be distinguished by the rate of release of $P_i$ with molybdate-malachite green at 37 °C ($k_\beta/k_\alpha$ 1.34 and 3.16, respectively).[617] Calorimetric measurements gave $\Delta H^\circ$ 1.40 kJ/mol (enthalpy) and $\Delta C_p^\circ$ −46 J/(mol K) (heat capacity) for the hydrolysis of Man6P with alkaline phosphatase.[383]

## Phosphorylation

Gal1P is phosphorylated by G1,6P in the presence of phosphoglucomutase, cysteine, and Mg(II), giving G6P and (presumably) Gal1,6P. The rate is somewhat slower than that for ribose 1-phosphate.[618]

## Separation and Analysis

Gal1P and Man6P may be separated from other phosphate esters and from each other by two-dimensional PC, TLC, PC/PE, or TLC/TLE (Table 1-9). Gal1P was determined in sugar beets by the consumption of ATP (luciferin-luciferase method) after conversion to F6P with a mixture of Gal1P uridyltransferase, PG mutase, and PG isomerase (Fig 1-5, steps 19, 2, and 3).[481]

## Structure

The preferred conformation of the pyranose ring of the 1-phosphate in aqueous solution is $^4C_1$ with the $C_5$-$C_6$ bond in gt↔tg equilibrium for Gal1P and gg↔tg for Man1P.[461] Pure Gal6P is a mixture of α and β pyranose anomers in a 32:64% ratio with no more than 4% furanose forms. The ratio of pyranose anomers is the same (1:2) in aqueous solution.[602]

**Table 1-9** Galactose and Mannose Phosphates*

| No. | Plant part | Method | Gal1P | Gal6P | Man1P | Man6P | References |
|---|---|---|---|---|---|---|---|
| *Beta vulgaris* L. (Sugar Beet) | | | | | | | |
| 1 | Leaf[a] | PC/PC | | | | + | 483 |
| 2 | Axis[a,b] | Enzym. | 7.5-11.0 | | | | 481 |
| *Brassica pekinensis* (Lour.) Rupr. (Pe-tsai) | | | | | | | |
| 1 | Petiole vascular bundle | PC/PC | | | | + | 36 |
| 1 | Petiole vascular bundle | TLC/TLC | | | | + | 36 |
| 1 | Petiole vascular bundle | TLC/TLE | | | | + | 36 |
| *Brassica rapa* L. (Turnip Rape) | | | | | | | |
| 1 | Petiole vascular bundle | TLC/TLC | | | | + | 240 |
| *Cucumis sativus* L. (Cucumber) | | | | | | | |
| 1 | Root | PC | + | | | | 619 |
| *Cucurbita maxima* Duch. (Hubbard Squash) | | | | | | | |
| 1 | Leaf sieve tube exudate | TLC/TLC | | | | + | 240 |
| *Hemerocallis* hybrid (Day Lily) | | | | | | | |
| 1 | Flower petal | TLC/TLC | | | | + | 266 |
| *Larix decidua* Mill. (European Larch) | | | | | | | |
| 1 | Cambial sap | IEC/PC | | tr | | | 504 |
| *Lycopersicon esculentum* Mill. (Tomato) | | | | | | | |
| 1 | Fruit | TLE | + | | | | 589 |
| *Prunus armeniaca* L. (Apricot) | | | | | | | |
| 1 | Leaf | PC/PC | | | | 17.3 | 397 |
| 1 | Leaf[a] | PC/PE | | | | 14.2 | 37 |
| *Solanum tuberosum* L. (Potato) | | | | | | | |
| 1 | Tuber[a] | PC/PC | | | | 13 | 314 |
| *Spirodela oligorrhiza* (Kurz.) Hegelm. (Duckweed) | | | | | | | |
| 1 | Whole plant | PC/PC | | ~40 | | 120 | 327 |
| *Zea mays* L. (Corn) | | | | | | | |
| 1 | Root[c] | PC | 550 | | | | 619 |

*nmol/g fresh weight basis unless stated otherwise.
[a]Basis unstated.
[b]nmol/axis.
[c]µg/g.

# Heptose Phosphates

This group comprises two sedoheptulose phosphates, Se7P and Se1,7P, and one manno-heptulose phosphate, Ma7P.

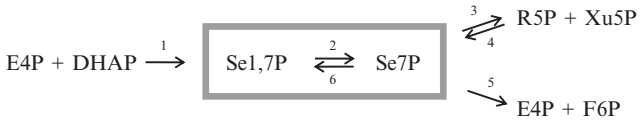
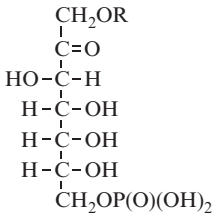
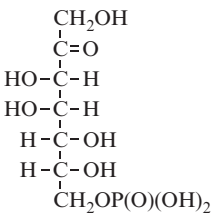



**FIGURE 1-7 Heptose Phosphates**. (1) Aldolase [E.C. 4.1.2.13]. (2) Sedoheptulose 1,7-bisphosphatase [E.C. 3.1.3.37]. (3, 4) Transketolase [E.C. 2.2.1.1]. (5) Transaldolase [E.C. 2.2.1.2]. (6) F6P kinase [E.C. 2.7.1.11], ATP.




**Se7P**, R = H
**Se1,7P**, R = $P(O)(OH)_2$




**Ma7P**

D-Sedoheptulose 7-Phosphate, $C_7H_{15}O_{10}P$; not listed in Beilstein. *D-altro-2-Heptulose 7-(Dihydrogen Phosphate)* [1951].

D-Sedoheptulose 1,7-Bisphosphate, $C_7H_{16}O_{13}P_2$; not listed in Beilstein. *D-altro-2-Heptulose 1,7-Bis(dihydrogen Phosphate)* [1963].

D-Mannoheptulose 7-Phosphate, $C_7H_{15}O_{10}P$: not listed in Beilstein. *D-manno-2-Heptulose 7-(Dihydrogen Phosphate)*, [1954].

## Occurrence

Se7P and Se1,7P are metabolites of the photosynthetic carbon reduction cycle (Calvin cycle) of higher plants (Fig. 1-7). In step 1, E4P undergoes an aldol condensation with DHAP, giving Se1,7P. In step 2, Se1,7P is hydrolyzed by sedoheptulose 1,7-bisphosphatase to Se7P and $P_i$. In step 3, Se7P transfers a two-carbon ketol segment to G3P, forming R5P and Xu5P. These reactions take place in the chloroplast, found only in the green leaf.

Se7P is also a metabolite of the respiratory pentose phosphate pathway. It is formed, together with G3P, by the interaction of R5P and Xu5P (step 4), and reacts with G3P to form E4P and F6P (step 5). These reactions take place in the cytoplasm, and in chloroplasts in periods of darkness.

A mannoheptulose phosphate, presumably the 7-ester, has been positively identified only in the avocado leaf,[517] but may be expected to occur in other plant species that have been shown to accumulate mannoheptulose.[620] Its metabolism is unknown. Mannoheptulose and its phosphate are both labeled rapidly upon brief photosynthesis in $^{14}CO_2$ but

the corresponding heptitol (perseitol), which occurs together with mannoheptulose in avocado, is not.[621]

## Physical Properties

D-Sedoheptulose 7-Phosphate

Se7P [R.N. 2646-35-7]: $[\alpha]_{589}^{22} + 4.65°$ (0.3*N*HBr),[622] $\Delta G°$ −253.2 kcal/mol.[84] Spectra: ORD,[622] GC/MS,[96] $^{13}$C NMR,[623] $^{31}$P NMR.[68] Chromatography: PC,[32] TLC,[105] IEC,[622] HPLC,[106] IC.[107] Electrophoresis: PE,[32] TLE,[105] zone,[88] isotachophoresis.[88]
$BaC_7H_{13}O_{10}P$: Amorphous solid.[622]

D-Sedoheptulose 1,7-Bisphosphate

Se1,7P [R.N. 815-91-8]: Faintly yellow sirup,[91] $\Delta G°$ −253.4 kcal/mol.[84] Spectra: $^{13}$C NMR,[623] $^{31}$P NMR.[68] Chromatography: TLC,[105] IEC,[624] HPLC.[26] Electrophoresis: TLE,[105] zone,[88] isotachophoresis.[88]
$Ba_2C_7H_{12}O_{13}P_2$: White solid.[91]

D-Mannoheptulose 7-Phosphate

Ma7P [R.N. 69975-90-2]: Spectra: $^{13}$C NMR, $^{31}$P NMR.[374] Chromatography: PC,[621] IEC.[345]

## Synthesis

Se7P may be prepared (a) by condensation of R5P with 2-nitroethanol,[622] (b) by the action of transaldolase-free enzyme preparations from spinach,[625] *Vicia faba*[626] or *Streptococcus faecalis* 10Cl[627] on R5P, (c) by the action of transketolase on a mixture of R5P and L-erythrulose, [628] or (d) by the action of Se1,7P diphosphatase on Se1,7P.[91] Enzymatic phosphorylation of sedoheptulose with hexokinase/ATP gives the 6-phosphate instead.[629] Se1,7P may be prepared by the action of aldolase and transketolase on a mixture of Se7P and F6P[625] or on a mixture of G3P and E4P.[91]

Ma7P may be prepared (a) by phosphorylation of methyl α-D-mannoheptuloside or di-*O*-isopropylidene-D-mannoheptulofuranose with diphenyl phosphorochloridate[374] or (b) by the action of transketolase on a mixture of arabinose-5-phosphate and Xu5P[345] or L-erythrulose.[628]

## Separation and Analysis

Se7P and Se1,7P can be separated from other phosphate esters by IEC or HPLC and identified by the Dische method,[19] by TLC/TLE,[20] or by retention time[26,106] (Table 1-10). In many cases, the heptose phosphates have been separated by two-dimensional PC and their identities confirmed by PC of the free sugars after enzymatic dephosphorylation.

Se7P and Se1,7P have also been determined directly on PCA extracts without prior separation by enzymatic methods similar to those employed with F6P and F1,6P. Four

**Table 1-10** Heptose Phosphates in Plants*

| No. | Plant part | Method | Ma7P | Se7P | Se1,7P | References |
|---|---|---|---|---|---|---|
| *Beta vulgaris* L. (Sugar Beet) | | | | | | |
| 1 | Leaf[a] | PC/PC | | + | | 483 |
| *Brassica pekinensis* (Lour.) Rupr. (Pe-tsai) | | | | | | |
| 1 | Petiole vascular bundle | PC/PC | + | | | 36 |
| 1 | Petiole vascular bundle | TLC/TLC | + | | | 36 |
| 1 | Petiole vascular bundle | TLC/TLE | + | | | 36 |
| *Coleus blumei* Benth. (Painted Nettle) | | | | | | |
| 3 | Leaf | PC/PC | | + | | 630 |
| *Glycine max* (L.) Merr. (Soybean) | | | | | | |
| 1 | Leaf | HPLC | | | + | 26 |
| *Kalanchoë daigremontiana* Hammett et Perrier (Devil's Backbone) | | | | | | |
| 1 | Leaf[b] | Enzym. | | | 15 | 275 |
| *Persea gratissima* Gaertn. (Avocado) | | | | | | |
| 1 | Leaf | PC/PC | + | + | | 517 |
| *Pisum sativum* L. (Peas) | | | | | | |
| 1 | Leaf chloroplast | HPLC | | Low | + | 106 |
| *Populus gelrica* (Houtz.) Houtz. | | | | | | |
| 1 | Bark[c,d] | Enzym. | | 0.042 | | 298 |
| *Populus nigra* L. (Black Poplar) | | | | | | |
| 1 | Bark[c,d] | Enzym. | | 0.026 | | 298 |
| *Pyrus communis* L. (Pear) | | | | | | |
| 1 | Fruit skin | IEC | | + | | 19 |
| *Robinia pseudoacacia* L. (Black Locust) | | | | | | |
| 1 | Leaf | PC | | + | + | 631 |
| *Spinacia oleracea* L. (Spinach) | | | | | | |
| 1 | Leaf | PC/PC | | + | + | 321 |
| 1 | Leaf[b] | Enzym. | | | 12 | 632 |
| 1 | –, chloroplast[b,d] | IEC | | + | 2.15 | 20 |
| *Triticum aestivum* L. (Wheat) | | | | | | |
| 1 | 10-day leaf | PC/PC | | + | | 331 |
| *Vicia faba* L. (Broad Bean) | | | | | | |
| 1 | Leaf | PC/PC | | + | + | 321 |
| *Vigna mungo* (L.) Hepper (Black Gram) | | | | | | |
| 1 | Seedling | PC | | + | | 631 |
| 1 | –, hypocotyl tip | Enzym. | | 2.2 | | 332 |

*nmol/g fresh weight basis unless stated otherwise.

[a]Air-dry basis.

[b]nmol/mg chlorophyll.

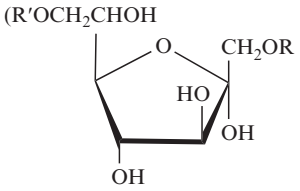
[c]Conc., m*M*.

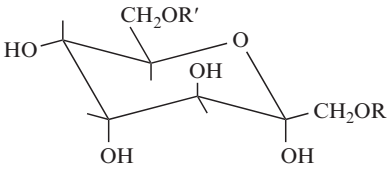
[d]Basis unstated.

different procedures were adopted for the compounds in Table 1-11, each capable of distinguishing sedoheptulose esters from fructose esters.

### Structure

In aqueous solution, both sedoheptulose phosphates exist as equilibrium mixtures of β-furanose, α-furanose (**18** and **20**), and α-pyranose (**19** and **21**) forms. The ratios for Se7P and Se1,7P are 67:17:16 and 74:13:13, respectively.[623] Ma7P exists exclusively as the α-pyranose in aqueous solution[374]:



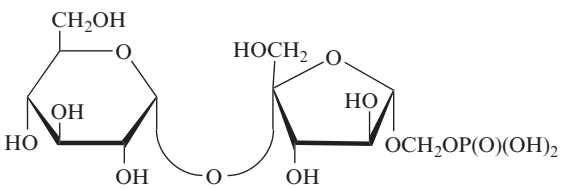

**18**, R = H, R′ = $P(O)(OH)_2$
**20**, R = R′ = $P(O)(OH)_2$

**19**, R = H, R′ = $P(O)(OH)_2$
**21**, R = R′ = $P(O)(OH)_2$

## Octose Phosphates

D-*altro*-2-Idooctulose 1,8-bisphosphate (Id1,8P), a metabolite of the pentose phosphate pathway in rat liver, was reported in a meeting abstract to be formed in spinach (*Spinacia oleracea* L.) leaf during brief photosynthesis in $^{14}CO_2$; its concentration in the chloroplast was about 1.3 nmol/mg chlorophyll.[633] No further details are available.

## Sucrose 6′-Phosphate




Sucrose 6′-Phosphate, $C_{12}H_{23}O_{14}P$; not listed in Beilstein. *Sucrose 6-(Dihydrogen Phosphate)* [1953].

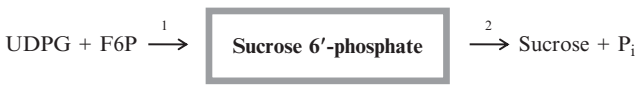



**FIGURE 1-8 Sucrose 6′-Phosphate.** (1) Sucrose phosphate synthase [E.C. 2.4.1.14]. (2) Sucrose phosphatase [E.C. 3.1.3.24].

## Occurrence

Sucrose 6′-phosphate is a metabolite in the synthesis of sucrose in the higher plants. It is formed by the reaction of UDPG with F6P and is hydrolyzed to sucrose by sucrose phosphatase (Fig. 1-8).

## Physical Properties

Sucrose 6′-Phosphate [R.N. 22372-29-8]: Spectra: $^{1}$H NMR (fig.).[634] Chromatography: PC,[635] IEC,[636] HPLC.[637] Electrophoresis: CE.[90]

$K_2C_{12}H_{21}O_{14}P{\cdot}3H_2O$: Microcrystalline solid, $[\alpha]_D^{20}$ +34° ($H_2O$).[549]

$BaC_{12}H_{21}O_{14}P{\cdot}3H_2O$: Amorphous solid, $[\alpha]_D^{20}$ +35.4° ($H_2O$).[549]

## Synthesis

Sucrose 6′-phosphate may be prepared (a) by phosphorylation of sucrose with sodium metaphosphate[634] or of sucrose 2,3,4,6,1′,3′,4′-heptaacetate with cyanoethyl phosphate/DCC[549] or (b) by reaction of UDPG with F6P catalyzed by sucrose phosphate synthase.[638]

## Hydrolysis

Sucrose 6′-phosphate is stable to alkali. Mild hydrolysis in 1*N* acid (5 min at 100 °C) yields D-glucose and F6P.[638]

**Table 1-11** Sucrose 6′-Phosphate in Plants*

| No. | Plant part | Method | Sucrose-6P | References |
|---|---|---|---|---|
| *Beta vulgaris* L. (Sugar Beet) | | | | |
| 1 | Leaf | PC/PC | + | 483 |
| *Camellia sinensis* L. Tea | | | | |
| 1 | Leaf | Enzym. | 0.1 | 488 |
| –, var.*assamica* (Mast.) Kitam. (Assam Tea) | | | | |
| 1 | Leaf | Enzym. | 0.5 | 488 |
| *Fragaria vesca* L. (Woodland Strawberry) | | | | |
| 1 | Leaf | Enzym. | 3.6 | 488 |
| *Pisum sativum* L. (Peas) | | | | |
| 1 | Cotyledon | Enzym. | 23 | 527 |
| *Ricinus communis* L. (Castor Bean) | | | | |
| 1 | Cotyledon | Enzym. | 52 | 303 |
| *Spinacia oleracea* L. (Spinach) | | | | |
| 1 | Leaf[a] | Enzym. | 0.6-0.7 | 637 |
| *Spirodela oligorrhiza* (Kurz.) Hegelm. (Duckweed) | | | | |
| 1 | Whole plant | PC/PC | 30 | 327 |

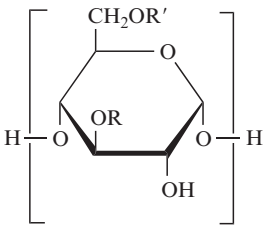
*nmol/g fresh weight basis unless stated otherwise.

[a]nmol/mg chlorophyll.

### Analytical Methods

The sucrose 6′-phosphate content of plant tissue is difficult to determine because of the presence of active sucrose synthase and phosphatase enzymes in the same tissue and low levels of the metabolite. In early work it was determined by two-dimensional PC and autoradiography after labeling with $^{14}C$ or $^{32}P$ (Table 1-11).[327,483] Later, it was determined by hydrolysis with 0.1*N* HCl at 100 °C and analyzed for F6P by fluorimetry.[488] In the enzymatic method, which is now preferred, the sucrose 6′-phosphate is isolated by IEC, hydrolyzed with alkaline phosphatase, and assayed for sucrose by coupled enzymatic assay.[527]

## Starch Phosphate




**Starch**, R = R′ = H
**Starch 6-Phosphate**, R = H, some R′ = $P(O)(OH)_2$
**Starch 3-Phosphate**, R′ = H, some R = $P(O)(OH)_2$

### Occurrence

It has long been known that starch contains a small amount of residual phosphorus that cannot be removed by extraction.[639] In some plants, such as the potato, the residual phosphorus is carbohydrate-bound whereas in others, such as wheat or corn, the residual phosphorus is lipid-bound. In this chapter we are concerned only with carbohydrate-bound phosphorus.

In the potato, the residual phosphorus seems to be confined to the amylopectin component of the starch. The amount is small—about one phosphorus for every 400 D-glucosyl residues.[640] About one third of the phosphorus is bound as glucose 3-phosphate and two thirds as glucose 6-phosphate.[641] The phosphate level is independent of potato variety for C-3 but not for C-6, and as a consequence the C-6 to C-3 ratio varies from 2.0:1 to 3.4:1.[642]

The phosphate group in the amylopectin protects the 1→4 α-D-glucosidic linkages in its vicinity from attack by amylase in a manner similar to the protection afforded by the 1→6 α-D-glucosidic branch points. Both the crystallinity[643] and enthalpy of gelatinization[644] of the native starch decrease with increasing phosphorylation. These results are consistent with the fact that the C-3 carbons face the interior of the amylopectin helix whereas the C-6 carbons face the exterior, insulating the former and exposing the latter to interaction with other molecules.[643]

**Table 1-12** Residual Phosphorus Content of Starch*

| No. | Plant part | P ($G_3P$) | P ($G_6P$) | P (total) | References |
|---|---|---|---|---|---|
| *Aesculus hippocastanum* L. (European Horse Chestnut) | | | | | |
| 1 | Nut, amylopectin | | | 0.015 | 650 |
| *Amaranthus hypochondriacus* L. (Prince's Feather) | | | | | |
| 1 | Waxy seed | | 0.003[a] | 0.003 | 651 |
| *Amorphophallus campanulatus* (Roxb.) Blume ex Deane (Telingo Potato) | | | | | |
| 1 | Corm, amylopectin | | | 0.044 | 650 |
| *Arenga pinnata* (Wurmb.) Merr. (Sugar Palm) | | | | | |
| 1 | Pith, amylopectin | | | 0.015 | 650 |
| *Arum maculatum* L. (Cuckoopint) | | | | | |
| 1 | Root, amylopectin | | | 0.014 | 650 |
| *Avena sativa* L. (Oats) | | | | | |
| 1 | Seed | | n.d.[a] | 0.056 | 651 |
| *Canna indica* L. (Indian Shot) | | | | | |
| 1 | Root | | | 0.044 | 652 |
| 1 | –, amylopectin | | | 0.106 | 650 |
| *Castanea sativa* Mill. (Spanish Chestnut) | | | | | |
| 1 | Seed, amylopectin | | | 0.007 | 650 |
| *Colchicum autumnale* L. (Autumn Crocus) | | | | | |
| 1 | Corm, amylopectin | | | 0.007 | 650 |
| *Colocasia antiquorum* Schott. (Culcas, Egyptian Taro) | | | | | |
| 1 | Corm, amylopectin | | | 0.006 | 650 |
| *Colocasia esculenta* (L.) Schott. (Taro) | | | | | |
| 1 | Corm | | 0.022 | 0.027 | 653 |
| 1 | –, amylopectin | | | 0.018 | 650 |
| *Curcuma longa* L. (Turmeric) | | | | | |
| 1 | Root | | 0.186 | | 654 |
| 1 | –, amylopectin | Chain length distribution | | | 654 |
| 1 | Rhizome, amylopectin | | | 0.123 | 650 |
| *Curcuma viridiflora* Roxb. | | | | | |
| 1 | Rhizome, amylopectin | | | 0.053 | 650 |
| *Cyperus esculentus* L. (Yellow Nutsedge) | | | | | |
| 1 | Tuber, amylopectin | | | 0.031 | 655 |
| 1 | –, dextrin | | | 0.020 | 655 |
| *Cyperus rotundus* L. (Purple Nutsedge) | | | | | |
| 1 | Tuber, amylopectin | | | 0.0045 | 655 |
| 1 | –, dextrin | | | 0.048 | 655 |
| *Fagopyrum esculentum* L. (Buckwheat) | | | | | |
| 1 | Seed, amylopectin | | | 0.003 | 650 |
| *Glycine max* (L.) Merr. (Soybean) | | | | | |
| 1 | Cotyledon | | 0.008 | 0.013 | 653 |
| *Hordeum vulgare* L. (Barley) | | | | | |
| 1 | Seed | | | 0.059 | 656 |
| 1 | –, amylose | | | 0.001 | 656 |
| 1 | –, amylopectin | | | 0.041 | 656 |
| *Ipomeoa batatas* (L.) Lam. (Sweet Potato) | | | | | |

**Table 1-12** Residual Phosphorus Content of Starch*—cont'd

| No. | Plant part | P ($G_3P$) | P ($G_6P$) | P (total) | References |
|---|---|---|---|---|---|
| 1 | Tuber | | 0.008 | 0.012 | 653 |
| 1 | –, amylopectin | | | 0.0027 | 655 |
| 1 | –, dextrin | | | 0.0024 | 655 |
| *Ipomoea purga* Hayne (Jalap) | | | | | |
| 1 | Tuber, amylopectin | | | 0.006 | 650 |
| *Iris* spp. (Iris) | | | | | |
| 1 | Rhizome, amylopectin | | | 0.048 | 640 |
| *Lens culinaris* Medik. (Lentil) | | | | | |
| 1 | Seed | | 0.002[a] | 0.008 | 657 |
| 1 | –, amylopectin | | | 0.004 | 650 |
| *Malus domestica* Borkh. (Apple) | | | | | |
| 1 | Fruit, amylopectin | | | 0.025 | 640 |
| *Mangifera indica* L. (Mango) | | | | | |
| 1 | Seed, amylopectin | | | 0.012 | 640 |
| *Manihot esculenta* Crantz (Cassava) | | | | | |
| 1 | Root | | 0.008 | | 654 |
| 1 | Tapioca | | 0.008[a] | 0.008 | 651 |
| 2 | Tapioca | | | 0.005-0.018 | 658 |
| 1 | Tapioca | | | 0.060 | 659 |
| 1 | –, amylose | | | 0.018 | 659 |
| 1 | –, amylopectin | | | 0.026-0.030 | 659 |
| *Maranta arundinacea* L. (Arrowroot) | | | | | |
| 1 | Root | | 0.021[a] | 0.021 | 651 |
| 1 | –, amylopectin | | | 0.017 | 650 |
| 1 | –, amylopectin | Chain length distribution | | | 654 |
| *Metroxylon sagu* Rottb. (Sago Palm) | | | | | |
| 1 | Pith | | | 0.012 | 652 |
| 1 | –, amylopectin | | | 0.016 | 650 |
| *Musa paradisiaca* L. (Plantain) | | | | | |
| 1 | Fruit, amylopectin | | | 0.022 | 650 |
| *Nelumbo nucifera* Gaertn. (Sacred Lotus) | | | | | |
| 1 | Seed | | 0.005[a] | 0.005 | 651 |
| *Oryza sativa* L. (Rice) | | | | | |
| 6 | Nonwaxy seed | | | 0.014-0.032 | 660 |
| 1 | Nonwaxy seed | | 0.013[a] | 0.065 | 651 |
| 7 | Nonwaxy seed | | | 0.012-0.005 | 661 |
| 7 | –, amylose | | | 0.0024-0.0084 | 661 |
| 7 | –, amylopectin | | | 0.0017-0.0080 | 661 |
| 7 | –, amylopectin | Chain length distribution | | | 654 |
| 1 | Waxy seed | | 0.003[a] | 0.005 | 651 |
| 2 | Waxy seed | | | 0.001-0.002 | 660 |
| 1 | –, amylopectin | | | 0.0011 | 661 |
| *Oxalis purpurata* Jacq. | | | | | |
| 1 | Tuber, amylopectin | | | 0.0047 | 655 |
| 1 | –, dextrin | | | 0.0045 | 655 |

*Percentage, dry weight basis. [a]Total sugar phosphorus.

*Continued*

**Table 1-12** Residual Phosphorus Content of Starch*—cont'd

| No. | Plant part | P ($G_3P$) | P ($G_6P$) | P (total) | References |
|---|---|---|---|---|---|
| *Panicum miliaceum* L. (Proso Millet) | | | | | |
| 1 | Seed | | | 0.043 | 662 |
| *Pastinaca sativa* L. (Parsnip) | | | | | |
| 1 | Seed, amylopectin | | | 0.054 | 640 |
| *Pennisetum glaucum* R. Br. (Cattail Millet) | | | | | |
| 1 | Seed | | n.d.[a] | 0.058 | 651 |
| *Phalaris canariensis* L. (Canary Grass) | | | | | |
| 1 | Seed | | | 0.15 | 663 |
| *Phaseolus lunatus* L. (Lima Bean) | | | | | |
| 1 | Bean | 0.006 | 0.005 | 0.011 | 651 |
| *Phaseolus vulgaris* L. (Bean) | | | | | |
| 1 | Bean, amylopectin | | | 0.005 | 650 |
| *Pisum sativum* L. (Pea) | | | | | |
| 1 | Seed | 0.001 | 0.003 | 0.006 | 651 |
| 1 | –, amylopectin | | | 0.003 | 650 |
| *Pueraria hirsuta* Matsum. (Kudzu) | | | | | |
| 1 | Root | | 0.005 | 0.009 | 653 |
| *Raphanus sativus* L. (Winter Radish) | | | | | |
| 1 | Root, amylopectin | | | 0.025 | 650 |
| *Sagittaria trifolia* L. (Chinese Arrowhead) | | | | | |
| 1 | Root | | | 0.009 | 664 |
| *Secale cereale* L. (Rye) | | | | | |
| 1 | Seed | | | 0.025 | 665 |
| *Solanum phureja* Juz. and Buk. (Nightshade) | | | | | |
| 1 | Tuber | + | 0.078 | | 649 |
| *Solanum tuberosum* L. (Potato) | | | | | |
| 26 | Tuber | | 0.025-0.078 | | 666 |
| 2 | Tuber | Variation in $G_6P$ content from cortex to pith | | | 666 |
| 2 | Tuber | Variation in $G_6P$ content with tuber diameter | | | 319 |
| 7 | Tuber | | | 0.078-0.096 | 667 |
| 1 | Tuber | | 0.053 | 0.075 | 653 |
| 1 | Tuber, amylopectin | | 0.032 | 0.048 | 653 |
| 1 | –, amylose | | | 0.0009 | 668 |
| 1 | –, amylopectin | | | 0.076 | 668 |
| 1 | –, α-limit dextrin | $G_3P/G_6P$ ratio 1:4 | | | 669 |
| *Sorghum bicolor* (L.) Moench (Sorghum) | | | | | |
| 1 | Seed | | 0.003 | | 654 |
| *Trapa natans* L. (Water Chestnut) | | | | | |
| 1 | Seed | | 0.004[a] | 0.004 | 651 |
| *Triticosecale* Witt. (Triticale) | | | | | |
| 1 | Seed | | | 0.031 | 665 |
| *Triticum aestivum* L. (Wheat) | | | | | |
| 1 | Seed | | 0.001[a] | 0.054 | 651 |
| 1 | Seed | | | 0.118 | 659 |
| 1 | –, amylose | | | 0.018 | 659 |

**Table 1-12** Residual Phosphorus Content of Starch*—cont'd

| No. | Plant part | P ($G_3P$) | P ($G_6P$) | P (total) | References |
|---|---|---|---|---|---|
| 1 | –, amylopectin | | | 0.116-0.154 | 659 |
| *Vicia faba* L. (Broad Bean) | | | | | |
| 1 | Bean, amylopectin | | | 0.017 | 640 |
| *Vicia* spp. (Vetch) | | | | | |
| 1 | Tuber, amylopectin | | | 0.033 | 655 |
| 1 | –, dextrin | | | 0.005 | 655 |
| *Vigna radiata* (L.) Wilcz. (Mung Bean) | | | | | |
| 1 | Bean, amylopectin | 0.004 | 0.007 | 0.012 | 651 |
| *Zea mays* L. (Maize) | | | | | |
| 1 | Seed | | | 0.017 | 670 |
| 1 | Seed | | tr[a] | 0.016 | 651 |
| 1 | –, amylose | | | 0 | 671 |
| 1 | Waxy seed | | 0.002 | 0.002 | 651 |
| 1 | –, high amylose | | 0.013[a] | 0.020 | 651 |

*Percentage, dry weight basis.

[a]Total sugar phosphorus.

## Hydrolysis

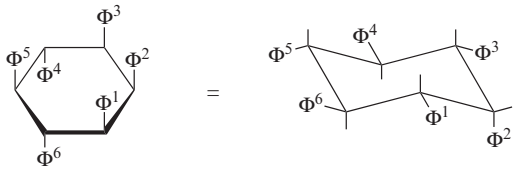
Enzymatic degradation of potato starch with amylase yields mixtures of phosphorylated oligosaccharides (phosphodextrins) of varying chain length, depending on the nature of the amylose and the severity of the reaction conditions. With few exceptions, the phosphodextrins are linear, contain one phosphate group per mole, and have at least one unsubstituted glucosyl residue at the reducing end.

The smallest phosphodextrins obtained by this method are maltose 6-phosphate,[641] maltotriose $6^2$-phosphate,[645,646] maltotetraose $6^3$-phosphate,[647,648] maltopentaose 6-phosphate,[646] and maltohexaose $6^3$-phosphate,[647] where the superscript denotes the glucosyl residue bearing the phosphate substituent counting from the reducing end (right end in the formula illustrated above). All are prepared by treatment of potato starch with α-amylase to the limit of enzymatic hydrolysis, followed in some cases by further hydrolysis with β-amylase or mineral acid. Digestion of potato starch with α-amylase alone yields a series of phosphodextrins from pentaose through octaose (separated by paper chromatography) which contain progressively more phosphate on C-3.[645]

The ester linkage in starch 3-phosphate is somewhat acid-labile, which makes it difficult to quantify.[649] Tabata and Hizukuri[641] found evidence for an even more acid-labile phosphate in potato starch (approximately 1% of the phosphate in the starch), possibly as glucose 2-phosphate, but this has yet to be confirmed.

The residual phosphorus content of starch in various plants and the distribution between glucose 3-phosphate and glucose 6-phosphate if known is given in Table 1-12.

# 2 Phytic Acid




Phytic acid, $\Phi$ = $OP(O)(OH)_2$

Phytic Acid ($InsP_6$), $C_6H_{18}O_{24}P_6$; Beilstein **6**H 1197, $E_I$ 590, $E_{II}$ 1160, $E_{III}$ 6935, $E_{IV}$ 7927. myo-*Inositol Hexakis(dihydrogen phosphate)* [1872]

## Occurrence

Phytic acid, the hexaphosphate ester of *myo*-inositol, is found in all plant seeds, being most abundant in the cereals and legumes. It occurs frequently in the form of a calcium magnesium salt for which Posternak[672] coined the name "phytin" [R.N. 3615-82-5]. Some plant phytins, however, contain more potassium than calcium, and other elements may be present such as Mn, Fe, or Zn.[673] Phytin, therefore, is not a definite compound but a collective term for the various salt forms of phytic acid in its natural state.

Phytic acid was isolated from wheat seed by Pfeffer[674] in 1872 and identified as an ester of *myo*-inositol and phosphoric acid by Winterstein[675] in 1897, but its structure was not established unambiguously until much later.

For general references on this subject see Cosgrove and Irving[676] or Graf.[673]

## Physical Properties

Phytic Acid [R.N. 83-86-3]: Thick, practically colorless syrup that darkens on standing or on heating to 100 °C or above[677]; $d^{25}$ 1.369,[678] $[\alpha]_D^{20}$ 0.00 ($H_2O$)[679]; soluble in water and acetone, slightly soluble in methanol and ethanol, and insoluble in ether, hexane, benzene, chloroform, and glacial acetic acid[678,680]; p$K_a$ −0.15 ($P_2$) to 11.76 ($P_{1,3}$ and $P_{4,6}$), all 12 p$K_a$s assigned[681]; conductivity.[682] Spectra: UV (fig.),[683] IR,[679,684] near IR,[685] Raman,[686] $^1$H NMR, [687] $^{13}$C NMR,[686] $^{31}$P NMR,[679,686,688] HMQC $^{31}$P NMR (fig.),[689] FAB/MS,[690] ESR.[691] Chromatography: PC,[692] TLC,[693] IEC,[694] HPTLC,[407] GFC,[695] HPLC,[696] IC.[697] Electrophoresis: PE,[698] TLE,[693] disk gel,[699] CZE.[700]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$Na_{12}C_6H_6O_{24}P_6{\cdot}38H_2O$ [R.N. 14306-25-3]: Colorless rhombic prisms, mp 58-59 °C,[701,702] soluble in hot $H_2O$, insoluble cold,[702] piezoelectric positive[701]; X-ray, d 1.75[701,703]; loses $35H_2O$ at 120 °C giving a trihydrate, white amorphous solid, dec. 210 °C.[702]

$Na_{12}C_6H_6O_{24}P_6{\cdot}nH_2O$: Hydrates of composition $n=1$[679]; $n=33$, X-ray, DTA, PE[679,704]; $n=35$, X-ray, DTA[679,704]; $n=47$[702]; $n=x$ (indefinite), solubility in $H_2O$[705] and aqueous ethanol[706]; near IR (fig.),[685] TGA,[707] Raman,[686] FAB/MS (positive and negative).[690]

$Ca_5C_6H_8O_{24}P_6{\cdot}3H_2O$ [R.N. 78342-17-3]: White amorphous powder, slightly soluble in $H_2O$[708]; solubility versus pH[709]; solubility product in 0.2 and 1.0*M* NaCl[710]; X-ray (fig.).[710]

$Ca_6C_6H_6O_{24}P_6{\cdot}xH_2O$ [R.N. 7776-28-5]: IR, Raman.[686]

$(C_{23}H_{26}N_2O_4)_6C_6H_{18}O_{24}P_6{\cdot}24H_2O$ (brucine salt): Needles, mp ~210-211 °C.[711]

$(C_{21}H_{22}N_2O_4)_6C_6H_{18}O_{24}P_6$ (strychnine salt): Slender needles, mp 203-204 °C,[712] ~210-211 °C,[711] or 218-219 °C.[713]

## Synthesis

Phosphorylation of *myo*-inositol with phosphoric acid/phosphorus pentoxide at 130 °C yields a mixture of *myo*-inositol polyphosphates ($n=4$-6) from which phytic acid can be isolated by fractional crystallization of the barium salts. The yield is only 8%.[702] Alternatively, *myo*-inositol may be phosphorylated with polyphosphoric acid at 160 °C and purified by ion exchange chromatography.[714] Phosphoric acid[715] and pyrophosphoric acid[708] yield only partially phosphorylated products. Phosphorylation of *myo*-inositol with triethylammonium *N*-benzoylphosphoramidate in DMF followed by removal of the protecting groups gives phytic acid ($InsP_6$) together with a small amount of Ins (1,3,4,5,6)$P_5$. The protective reagents usually employed in the phosphorylation of alcohols are ineffective.[716]

## Hydrolysis

Hydrolysis of phytic acid under carefully controlled conditions leads to a series of *myo*-inositol derivatives ranging from pentakisphosphates to monophosphates. Owing to the unsymmetrical nature of the *myo*-inositol molecule, there are 6 possible pentakisphosphates, 15 tetrakisphosphates, 20 trisphosphates, 15 bisphosphates, and 6 monophosphates. Some of these are D,L-stereoisomer pairs, reducing the number of chemically distinct isomers to 4, 9, 12, 9, and 4, respectively.

Hydrolysis of phytic acid at 95 °C, measured by the release of $P_i$, follows first-order kinetics with a rate constant of $8.74\times10^{-4}$ $min^{-1}$ at pH 4, falling to $3.98\times10^{-4}$ at pH 1, and $0.28\times10^{-4}$ at pH 12. The presence of metal ions has little influence on the rate.[717]

Hydrolysis of phytic acid at pH 4.0 and 110 °C for 100 min in a sealed tube yields a pentakisphosphate fraction[718] that can be separated into its individual components by ion exchange chromatography[719] or moving paper electrophoresis.[720] The structures of the isomers (confirmed by later studies) are illustrated in Fig. 2-1.[719]

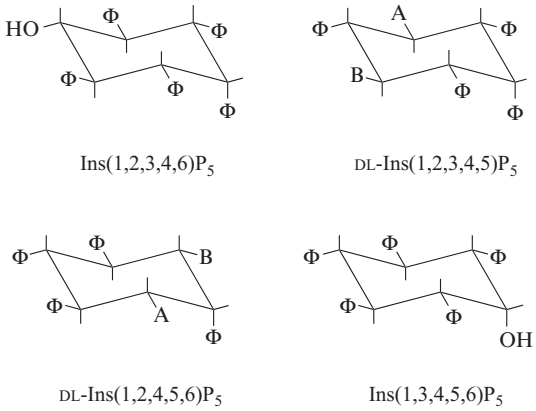


**FIGURE 2-1** *myo*-Inositol Pentakisphosphates. A = OH, B = Φ for the D isomer and A = Φ, B = OH for the L isomer.

Further hydrolysis of phytic acid with acid, base, or enzyme catalysts can be made to give tetrakis-, tris-, bis-, or monophosphates depending on the severity of the reaction conditions. The complexity of the mixtures does not permit the isolation of individual isomers until the monophosphate stage is reached. The only monophosphate formed under acid or base catalysis is the *meso* isomer Ins(2)P,[721,722] but some Ins(1)P is also formed under enzyme catalysis.[723]

Complete hydrolysis of phytic acid to *myo*-inositol and phosphoric acid requires more drastic conditions such as 8 h refluxing with 35% $H_2SO_4$[724] or autoclaving at 220-230 °C with 20% NaOH.[675] Phytase does not remove the last phosphate group.

## Conformation

The conformation of calcium phytate, like that of *myo*-inositol itself, is known to be $1_{ax}/-5_{eq}$ in the solid state, based on Raman spectroscopic analysis.[686] Sodium phytate, however, has the inverted $5_{ax}/1_{eq}$ conformation, based on X-ray diffraction measurements on the crystalline salt.[703]

The situation is much less clear for phytic acid and its salts in aqueous solution. According to $^{13}C$ NMR, $^{31}P$ NMR, and Raman spectroscopy, sodium phytate has the $1_{ax}/5_{eq}$ conformation at low pH and the $5_{ax}/1_{eq}$ conformation at high pH. The inversion occurs at pH 9.4.[686] The tetra-*n*-butylammonium salt exhibits three inversions: from $5_{ax}/1_{eq}$ to $1_{ax}/5_{eq}$ at pH 2 and at pH 12 and from $1_{ax}/5_{eq}$ to $5_{ax}/1_{eq}$ at pH 5.[688] The preferred conformation apparently depends on the nature of the counterion as well as the degree of protonation. That this matter remains unresolved is evident from two papers published in 1999 in which one group carried out a detailed study of an equatorial to axial inversion occurring in the pH 10-11.3 range[725] while another group, using the same reagents and spectroscopic methods, found no such inversion up to pH 12 (Fig. 2-2).[726]

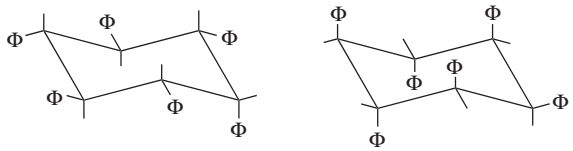

**FIGURE 2-2** Conformational isomers of phytic acid. Left, $1_{ax}/5_{eq}$ conformer; right, $5_{ax}/1_{eq}$ conformer. The unique substituent is at C2 in both cases. Note the steric crowding of the phosphate (Φ) groups in the $5_{ax}/1_{eq}$ conformer.

## Preparative Methods

Phytic acid can be isolated from the seeds of a variety of plant species by extraction with acid. Some of the sources for which detailed procedures have been described are listed in Table 2-1.

Despite the availability of several synthetic methods, phytic acid is seldom prepared by chemical synthesis since it is so readily available from natural sources. Commercial phytic acid is prepared from corn steep liquor in the United States[673c] and from rice bran in Japan.[678] Phytic acid solutions that contain salts can be desalted by ion exchange chromatography or more conveniently by dialysis.[729] Calcium precipitation is inefficient.[730]

**Table 2-1** Phytic Acid from Various Plant Sources

| Plant species | % Yield | References |
|---|---|---|
| *Brassica campestris* L. (Field Mustard) | 0.38-0.57 | 712 |
| *Acer saccharinum* L. (Silver Maple) | 0.49 | 727 |
| *Pisum sativum* L. (Peas) | 0.30 | 728 |
| *Triticum aestivum* L. (Wheat) | 0.14 | 713 |

## Quantitative Analysis

There are no known reagents specific for phytic acid. It does not have a characteristic UV, visible, or IR spectrum. Much attention, therefore, has been devoted to the development of suitable methods for its analysis. The more rigorous of these methods include hydrolysis of the phytic acid and separate analysis of its component parts: *myo*-inositol and phosphoric acid.

For many years, the most widely used method was that of Heubner and Stadler[731] in which phytic acid is precipitated as the sparingly soluble ferric salt (Fe:P ratio 4:6).[732] Several modifications of this method have been introduced and some have been widely adopted.[733–735] The lower limit of detection is ~3 μg/mL of phytate phosphorus.[736] In 1977, Harland and Oberleas[737] proposed an ion exchange chromatographic method that has since been adopted as an official AOAC standard.[738] In this method, an aliquot of the extract is transferred to a column containing a strong base anion exchange resin such as AG1-X4 (Cl form), eluted with NaCl in a gradient from 0.1 to 0.7*M*, digested with acid, and analyzed for %P. The use of reverse phase HPLC for the analysis of phytic acid proposed

by Tangendjaja *et al.*[739] in 1980 is becoming more and more widely used as modifications have been introduced to increase its accuracy and sensitivity.[740–742] Detection limits as low as 2 ng have been reported.[740] Other methods include $^{31}$P NMR,[743] polarography,[744] bioassay with phytase,[745] isotachophoresis,[746] ion chromatography,[697] near IR,[685] and kinetics of crystal growth.[747] Methods based on the analysis of the *myo*-inositol component include oxidation with periodic acid[724] and bioassay with *Schizosaccharomyces pombe*.[748]

*(1) McCance-Widdowson Method*

This method is a widely used modification of the ferric phytate method introduced by Heubner and Stadler in 1914, which was based on the insolubility of ferric phytate in the dilute acid used to extract the phytic acid from the plant.[731] The original method is now seldom used because of interference with other polyphosphates and with phosphoric acid, and because the endpoint of the titration is often difficult to determine precisely. In the McCance-Widdowson modification (1935), the ferric phytate is converted to sodium phytate, digested with perchloric acid, and analyzed for phosphorus:

> *5-10 g. of dried, finely-ground material were shaken in a small glass-stoppered bottle with 100 ml. N/2 HCl for 2 hours to extract the phytic acid; 10 to 40 ml. of the filtered extract were neutralized to phenolphthalein with NaOH, rendered slightly acid with HCl and made up to 50 ml. Duplicate 20 ml. aliquots were treated in 50 ml. centrifuge-tubes, with 4 ml. of the $FeCl_3$ solution [containing 0.5 mg. ferric iron per ml. of N HCl]. The tubes were heated in a boiling water bath for 15 min. to flocculate the precipitate of ferric phytate, cooled, centrifuged and the supernatant liquid poured off. The precipitate was washed with 5 ml. N/6 HCl, centrifuged again and the acid decanted. The precipitate was then stirred up with 2 ml. distilled water and heated in a boiling water bath for a few minutes. 2 ml. of 2% NaOH were then added, and the heating continued for a further 15 min. The solution containing the phytin as sodium phytate was filtered into a Kjeldahl flask, the precipitated ferric hydroxide was well washed with hot water and the washings were added to the filtrate in the flask. 1 ml. of conc. $H_2SO_4$ and 1 ml. of 65% $HClO_4$ were added, and the mixture incinerated very gently until completely digested. It was then heated strongly for 60 min. to drive off any residual $HClO_4$. When cool, about 20 ml. of water were added and the contents of the flask just neutralized to phenolphthalein with 40% NaOH. The solution was then made up to 100 ml. [and analyzed for phosphorus by the phosphomolybdate method].*
>
> Reproduced with permission from McCance, R. A.; Widdowson, E. M., "Phytin in Human Nutrition", *Biochem. J.* **1935**, *29*, 2694–2699,[735] © 1935 the Biochemical Society.

Some minor improvements have been described.[732,749–752] An alternative procedure is that of Young[753] in which the ferric ion is estimated calorimetrically, either in the precipitate[733,754] or in the supernatant solution.[734,753,754] As this method depends on the 6:4 stoichiometry of P:Fe in ferric phytate, much attention has been devoted to ensuring that the

ratio is correct. The most widely used variants of this method are those of Makower,[754] Young,[753] and Wheeler and Ferrel.[733] The Wade reagent used by Latta and Eskin[734] can be used if the phosphoric acid concentration does not exceed 20 mg/mL.[755] The lower limit of measurement in the McCance/Widdowson method is 0.16 mmol/mL.[746] The method has been semiautomated.[756]

### *(2) Michel-Durand Method*

This method was developed to overcome the coprecipitation of other phosphorus compounds, notably nucleic acids and sugar phosphates, with ferric phytate in the McCance/Widdowson method. In principle, the acid extract is treated with ammonia-magnesium reagent to precipitate inorganic and phytate P and the precipitate is dissolved in 0.5*N* HCl. Upon addition of calcium acetate, the phytate P precipitates but the inorganic P remains in solution.[757] In one study,[758] the calcium acetate treatment was omitted. Improvements in the Fe precipitation method (method 1) and the development of newer methods have rendered this method obsolete.

> *A volume of cold acid extract, equivalent to 200-300 g phytic P, is measured in a conical centrifuging tube; 2 ml. of magnesium reagent is added and the mixture is neutralized with 8* N *$NH_4OH$ in the presence of neutral red, then made alkaline with 1 ml. 8* N *$NH_4OH$. The precipitate is a mixture of crystalline MgNH, phosphate and amorphous Mg phytate. After standing overnight in the cold, it is separated by centrifugation, dissolved in 5 ml. 0.5* N *HCl, and immersed in a boiling-water bath for 10 min.; 5 ml. 25% Ca acetate is then added and the Ca phytate precipitate is heat-coagulated for 5 min. It is recovered by centrifuging and ashed for P determination.*
>
> Bourdet, A.; Feillet, P., "Distribution of Phosphorus Compounds in the Protein Fractions of Various Types of Wheat Flour", *Cereal Chem.* **1967**, *44*(5), 457–482,[759] reprinted by permission of AACC International, © 1967.

### *(3) Harland-Oberleas Method*

In this method, introduced in 1977, phytic acid is separated from phosphoric acid and any lower inositol phosphates by ion exchange chromatography, digested with concentrated $HNO_3$-$H_2SO_4$, and analyzed for phosphorus.[737]

> *Samples of dried material (5 g) were extracted for 2 hr at room temperature with 100 ml of 1.2 % HCl. . . . . Glass barrel Econo-columns (. . . . .0.7 x 15 cm) equipped with a 3-way Luer fit stop-cock. . . . .were clamped vertically and packed with about 0.5 g of 200-400 mesh AG1-X8 chloride form anion-exchange resin. . . . . Before use, the columns were washed first with 0.7* M *NaCl to assure chloride saturation of the resin and then with distilled water until the eluate was salt-free. The sample extract was diluted before being placed on the column so that the total anion concentration was less than 0.05* M *(about 1:25). The sample container was rinsed and the column*

> *was washed with 15 ml of distilled water to elute most of the inorganic phosphate. The remaining inorganic phosphate was eluted with 15 ml of 0.05* M *NaCl. The phytate was then eluted with 15 ml of 0.7* M *NaCl and collected in a microKjeldahl flask or digestion tube. To the digestion vessel was added 0.5 ml of concentrated $H_2SO_4$, 3.0 ml of concentrated $HNO_3$, and a few boiling chips. Digestion was continued until only the $H_2SO_4$ remained (25-30 min). . . . About 10-15 ml of distilled water was added to the digestion vessels, the contents were mixed thoroughly, and the vessels were placed in a boiling water bath for 15 min to hydrolyze any polyphosphates which may have formed during digestion. . . . . An aliquot of the digested eluate was then taken for phosphorus determination by the Fiske-Subbarow method.*
>
> Harland, B. F.; Oberleas, D., "A Modified Method for Phytate Analysis Using an Ion Exchange Procedure: Application to Textured Vegetable Proteins", *Cereal Chem.* **1977**, *54*(4), 827–832,[737] reprinted by permission of AACC International, © 1977.

To avoid digestion, many analysts prefer the modification of Latta and Eskin[734] in which the phytate content of the column eluate is determined spectrophotometrically with a modified Wade reagent (ferric chloride and sulfosalicylic acid, absorbance at 500 nm). One newer method measures the chloranilic acid released from zinc chloranilate by phytic acid at 332 nm,[760] another measures the fluorescence of 2,2′-dipyridyl ketone hydrazone after Cu(II)-catalyzed oxidation,[761] and yet another measures the molybdenum blue/phytic acid complex by flow injection analysis.[762] Analysis for phytate phosphorus without digestion is also possible with inductively coupled plasma spectrometry.[752] Minor improvements are the use of EDTA to remove interfering cations[763] and a more reliable resin (AG1-X4) for the ion exchange.[764] These changes are incorporated in the AOAC standard.[738]

### *(4) High-Performance Liquid Chromatography (HPLC) Method*

This method was introduced in 1978 by Gerritse,[696] who used it to measure the phytic acid content of a variety of organic materials including potatoes and annual bluegrass. Three variants of the method have evolved, one employing conventional ion exchange and the other two employing ion-pair and ion chromatography.

Cilliers and van Niekerk[765] developed a rapid, sensitive procedure that requires minimal sample preparation. It employs a low capacity anion exchange resin (IC-PAK-A), an isocratic mobile phase (0.045*M* $NaNO_3$/0.018*M* $HNO_3$), and postcolumn colorimetric detection with the Wade reagent ($FeCl_3$/sulfosalicylic acid). If hydrolysis of the phytic acid is suspected, the use of a linear gradient of 0-0.5*M* $NaNO_3$ in 0.01*M* 1-methylpiperazine provides a better separation of the lower inositol phosphates.[766] Strong anion exchange resins such as Aminex A-27 or PL-SAX can be employed provided that column hydrolysis is avoided by gradient elution with 0.1-0.5*M* NaCl containing $Na_4$EDTA.[767,768] Phytic acid can also be detected by the change in refractive index,[697] UV/vis spectrum,[697] or conductivity[769] of the eluate; by flame ionization (FID)[770]; or by evaporative light scattering (ELS).[771]

Early attempts to determine phytic acid by HPLC on reverse phase $C_{18}$ columns such as μBondapak or Spherisorb ODS were hampered by poor resolution owing to weak retention

on the column. Phytic acid eluted with the solvent front.[739–741,772] This problem was overcome by adding an ion-pairing reagent, tetrabutylammonium hydroxide, to the mobile phase[742] and by adjusting the pH to 4.3 to optimize the separation of the inositol tris-, tetrakis-, pentakis-, and hexakisphosphates.[773] In this procedure, the InsP's must be separated from the plant extract prior to injection into the HPLC column. The following procedure is typical:

> *Samples of 0.5 g freeze-dried, ground food or intestinal contents were extracted under vigorous mechanical agitation with 20 mL 0.5* M *HCl for 2 hr at 20 °C (Graf and Dintzis, 1982). The extract was centrifuged and the supernatant decanted, frozen overnight and filtered through MF-Millipore (0.22 μm) under pressure. The inositol phosphates were separated from the filtrate and concentrated by a modification of the ion-exchange procedure of Graf and Dintzis (1982). . . . The eluent was evaporated to dryness and diluted with 1 mL of water. . . . The mobile phase consisted of 0.05* M *formic acid:methanol (Fison HPLC grade) 49:51 and 1.5 mL/100 mL of TBA-OH (tetrabutylammonium hydroxide) (Fluka, 40 % in water) were added. The pH was adjusted to 4.3 by addition of 9* M *sulfuric acid. The mobile phase was filtered through a MF-Millipore (0.45 μm) under vacuum and degassed by sonication for 15 min. A reverse phase C-18 [HPLC] column (Waters Radialpak) 5 micron particle size was equilibrated with the mobile phase for 1 hr. Analysis was conducted with an HPLC pump (Waters Model 510) equipped with a Z-module. Inositol phosphates were detected by refractive index. . . . The optimal flow rate was 3 mL/min. Retention times and peak areas were measured. . . .*
>
> Sandberg, A.-S.; Ahderinne, R., "HPLC Method for Determination of Inositol Tri-, Tetra-, Penta- and Hexaphosphates in Foods and Intestinal Contents", *J. Food Sci.* **1986**, *51*(3), 547–550,[773] reprinted by permission of John Wiley & Sons, © 1985.

Lehrfeld[774,775] has introduced numerous modifications to improve the speed and reliability of the method. The third variant is ion chromatography, run in the isocratic mode with Dionex AS3 as the stationary phase and 0.11*M* $HNO_3$ as the mobile phase.[697] Treatment of the plant extract with EDTA eliminates the interference of metal ions.[776] The lower limit of detection for the HPLC method is reported to be 5 mg[696,741] to 2 ng[742] phytic acid at sample sizes down to 50 mg.[777]

### *(5) Gel Filtration Chromatography (GFC) Method*

Gel filtration chromatography (GFC) has been employed in a few instances to separate phytic acid from other plant phosphorus compounds. The column packing used most often is Sephadex G-25. The lower limit of detection is 0.05-0.5 mg phytate P/g.[696] Analysis of the phytate fractions for other elements in two of the cited references[778,779] (the third[696] used EDTA) revealed the presence of sodium, potassium, and magnesium but no calcium; this method therefore seems to offer a useful means for identifying the cationic components of plant phytins, a feature that should be further exploited.

### *(6) Near-Infrared Method*

Parrish *et al.*[685] recently developed a near-IR method for the analysis of phytic acid in cottonseed, using a pair of wavelengths (1568 and 1230 nm) selected from the 1100- to 2500-nm spectrum. The phytic acid content is calculated by means of the equation (% phytic acid $= 100.625 - 0.657\ (\lambda_{1568}/\lambda_{1230})$). The method is simple, rapid, and does not require prior extraction of the sample, but does require calibration for each plant substrate by one of the standard methods of analysis. The results correlated well ($R = 0.998$) with those determined for cottonseed by the HPLC method.[697] Nevertheless, Le Boever *et al.*[780] found the method to be of limited value for predicting the phytate content of 19 Belgian foodstuffs, even when split into starchy and protein-rich groups.

### *(7) $^{31}$P Nuclear Magnetic Resonance (NMR) Method*

In the pH 4-5 range, the $^{31}$P NMR spectrum of phytic acid exhibits a pattern of four signals in a 1:2:2:1 ratio that is readily distinguishable from those of inorganic phosphate and the lower inositol phosphates. In this method, introduced by O'Neill *et al.* in 1980, the peak area of one of these signals, usually the C-2 phosphate, is measured after a large number of transients by Fourier transform and compared to a calibrated standard[743]:

> *The sample (2.5 g) was stirred vigorously for 0.5 h in a solution of aqueous 3% w/v trichloroacetic acid (10 mL) containing 0.1% w/v sodium cyclotrimetaphosphate tetrahydrate at room temperature. . . . Additional 3% w/v trichloroacetic acid was used when necessary to ensure efficient stirring. After centrifuging, the supernatant was adjusted to pH 4.5 ± 0.5 by addition of tetrasodium EDTA before filtering (0.45-μm Millipore) and adding 2 mL to sucrose (2.5 g) with stirring to aid dissolution. . . . All spectra were recorded with proton noise-decoupling on a JEOL PFT-100 NMR spectrometer fitted with a 5-kHz crystal filter. The calibration and sample spectra were recorded [at 40.3 MHz, pulse width 15 ms, data acquisition time 1.02 s, deuterium lock. . . the] standard and phytate C-2 phosphate peak areas were calculated from the triangulated signals resulting from peak extrapolation on these spectra.*
>
> O'Neill, I. K.; Sargent, M.; Trimble, M. L., "Determination of Phytate in Foods by Fourier Transform Phosphorus-31 Nuclear Magnetic Resonance Spectrometry", *Anal. Chem.* **1980**, *52*(8), 1288–1291,[743] reprinted by permission of the American Chemical Society, © 1980.

The method was modified by Mazzola *et al.*[781] and Ersöz *et al.*,[782] who eliminated the need for sucrose as a relaxation agent by using phosphorous acid[782] or phytic acid itself[781] as the standard. Unlike other methods this method is specific for phytic acid, but it requires large sample sizes (2.5-5.0 g) and its sensitivity to samples of low phytate content (<0.1%) is poor.

### *(8) Inositol Method*

In this method, phytic acid is determined by bioassay of the *myo*-inositol liberated after hydrolysis with 1*N* HCl in a sealed Pyrex tube at 123 °C. *myo*-Inositol itself is stable under

these conditions. The results must be corrected for any free *myo*-inositol present in the plant tissue, which is determined separately by bioassay after extraction with 0.04*N* HCl at 4-5 °C[748]:

> *About 100 mg. of sample was heated with 2 ml. of* N*-HCl in a sealed Pyrex tube at 123° for 48 h. After cooling, the tube was opened, the hydrolysate filtered with numerous washings into a measuring flask, the pH adjusted to 4.8 with NaOH and the solution made up to volume. . . . The method used [to assay inositol] was described by Norris & Darbre (1956). The test organism was a strain of* S. pombe*. . . . The method is, in general, accurate within ±3%.*
>
> Reproduced with permission from Darbre, A.; Norris, F. W., "Vitamins in Germination. Determination of Free and Combined Inositol in Germinating Oats", *Biochem. J.* **1956**, *64*(3), 441–446,[748] © 1956 the Biochemical Society.

Free *myo*-inositol may also be determined by bioassay after prior separation from its phosphates, including phytic acid, by ion exchange chromatography on Amberlite IRA-410 ($OH^-$).[783] The bioassay organism may be *S. pombe*[784] or *Saccharomyces carlsbergensis*.[783] Alternatively, free *myo*-inositol may be determined by GC using scillitol as an internal standard.[785]

### *(9) Phytase Method*

This method, used extensively in Sweden for the analysis of phytic acid in rapeseed, is based on the hydrolysis of phytic acid by the enzyme phytase (E.C. 3.1.3.26). Since this method measures the $P_i$ released, and wheat phytase hydrolyzes only five of the six phosphate groups of phytic acid *in vitro*,[786] it would seem that the values should be low by a factor of 1/6 (16.7%), but direct comparison shows that the values are actually slightly higher than those of the Wheeler and Ferrel method.[745]

> *Defatted RSM [rapeseed meal] (1 g) was extracted with 25 ml 15% trichloroacetic acid (TCA) for 1 h at room temperature with mechanical shaking. After filtering, 6 ml of the solution was transferred to a 25-ml volumetric flask. Sodium acetate buffer (4 ml, 2.8* M*) containing 0.1* M *magnesium sulphate and 3 ml of [freshly prepared wheat] phytase solution was added. . . . The mixture was diluted to volume with distilled water, after which the pH was 5.1. Then 1 ml of this solution was taken and used for background phosphate analysis, and the remainder of the solution incubated for 16 h at room temperature. Thereafter, 1 ml of the hydrolysed solution was analyzed for phosphate by the ammonium molybdate method. The content of phytate phosphorus [was] calculated from the difference between the measurement before and after the enzymatic hydrolysis.*
>
> Uppström, B.; Svensson, R., "Determination of Phytic Acid in Rapeseed Meal", *J. Sci. Food Agric.* **1980**, *31*(7), 651–656,[745] reprinted by permission from John Wiley & Sons, © 1980.

### *(10) Paper Electrophoresis (PE) Method*

Phytic acid is readily separated from phosphoric acid and the lower inositol phosphates by paper electrophoresis.[787] The following method was adopted for the quantitative determination of phytic acid in pollen:

> *Dry pollen (200 mg) was ground in a mortar precooled with liquid $N_2$, then 2 ml 0.02* M *$Na_4EDTA$ was added, allowed to freeze over the pollen and the whole ground into a fine powder. The powder was allowed to thaw, with further grinding, poured into a small tube and heated in a boiling water bath for 20 min. After cooling to 0° [and] centrifugation (Sorvall SSI; 6000 g for 20 min)... the first... pellet was re-extracted... with 2 ml 0.02* M *$Na_4EDTA$.... Both [extracts] were subjected to paper electrophoresis (0.1* M *oxalic acid, pH 1.5; 550 V for 2 hr; on Whatman 3 MM paper 10 x 43 cm). Under these conditions phytic acid migrates well ahead of other cellular phosphate esters.... Phosphate-containing areas in the dry electrophoretogram were then stained by dipping in an acid molybdate solution in acetone... dried overnight in the dark and exposed briefly to sunlight next day. The intensity of the discrete blue spot from pollen extracts with the same mobility as phytic acid, was compared with that from a series of standard phytic acid spots run under the same conditions. It was found that as little as 1 nmol phytic acid (6 nmol of phosphate) could be detected by this method.*
>
> Jackson, J. F; Jones, G.; Linskens, H. F, "Phytic Acid in Pollen", *Phytochemistry* **1982**, *21*(6), 1255–1258,[788] reprinted by permission of Elsevier, © 1982.

Williams[789] cut out the phytate spots and digested them in Kjeldahl flasks with 70% (w/v) perchloric acid for P analysis by the Bartlett method.

### *(11) Capillary Zone Electrophoresis Method*

In this method, phytic acid is separated from phosphoric acid and the lower inositol phosphates by capillary zone electrophoresis (CZE), using appropriate buffers. The procedure of Blatny *et al.*[700] enables $InsP_6$, $InsP_5$, and $P_i$ to be analyzed in a single run. Others used potential gradient detection[746] or indirect UV detection with histidine as the UV absorber.[790]

> *Two to five grams of the ground sample is weighed into a 100 mL volumetric flask, and 50 mL of HCl of different concentrations (0-5%) is added. IP6 is extracted from the sample by shaking for 1 h at room temperature. After this period, the mixture is filtered, diluted, and directly analyzed by isotachophoresis. The volume-coupling instrument (Ionosep 900.1, Recman-Laboratorni Technika, Ostrava, Czech Republic) was equipped with Teflon capillaries.... Detection was carried out with a contactless high-frequency conductivity cell. The following constant current was applied: ... initially 70 mA (15 mA during detection).... The electrolyte system consist[ed] of*

*0.01 mol/L hydrochloric acid, 0.0056 mol/L bis-tris-propane (pH 6.1) as leading electrolyte, and 0.005 mol/L 2-morpholinoethanesulfonic acid as terminating electrolyte. . . . The detection limit was less than $10^{-6}$ mol/L, which corresponds to a phytic acid content of the samples of less than 0.08 %.*

Blatny, P.; Kvasnicka, F.; Kenndler, E., "Determination of Phytic Acid in Cereal Grains, Legumes, and Feeds by Capillary Isotachophoresis", *J. Agric. Food Chem.* **1995**, *43*(1), 129–133,[700] reprinted by permission of the American Chemical Society, © 1995.

### *(12) Other Quantitative Methods*

Miscellaneous other methods used for the analysis of phytic acid are outlined in Table 2-2. In some cases insoluble salts other than Fe (McCance method) or Mg (Michel method), such as the Ca,[708] Ba,[715,806] or Cu[708,807] salts, were used for the precipitation of phytate. The highly insoluble thorium[808] and bismuth[809] salts have been suggested but have not been used for this purpose. Babakhodzhaeva *et al.*[744] titrated a lead nitrate solution with a rice flour extract and determined its phytic acid content by polarography. In some cases the method was undisclosed or could not be determined.

**Table 2-2** Other Quantitative Methods

| Author | Method | References |
|---|---|---|
| Schmalfuss (1940) | $NH_4$ citrate extn., Cu acetate pptn. | 791,792 |
| Mukhamedova *et al.* (1977) | $HNO_3$ extn., pptn. of phytin | 793–796 |
| Suzuki (1907) | P (HCl-soluble) – $P_i$ | 797–799 |
| Ogawa *et al.* (1975) | P (total) | 800 |
| Ogawa *et al.* (1977) | P (acid-soluble) | 801 |
| Fontaine *et al.* (1946) | P (total) – $P_i$ | 802 |
| Kazakov *et al.* (1980) | $H_2O$ extn., pptn. of phytin | 803 |
| Morton *et al.* (1964) | P (total) – P (lipid) – P (nucleic acid) | 804,805 |

## Qualitative Analysis

### *(1) Chromatographic Methods*

Paper chromatography (PC) and thin layer chromatography (TLC) have been employed in a few instances for the identification of phytic acid in plant extracts. Sobolev[810] and others used *n*-PrOH/$NH_3$/-$H_2O$ (5:4:1) to separate phytic acid from $P_i$ and the lower inositol phosphates (see Chapter 3, Table 3-2)[693,811,812] and from other phosphate esters such as ATP or phosphatidylinositol (PI).[813] Other solvent mixtures have been used to separate phytic acid from inorganic polyphosphates[814] and sugar phosphates.[315]

### *(2) Disk Gel Electrophoresis (DGE) Method*

Polyacrylamide disc gel electrophoresis of aqueous seed extracts has been used to verify complex formation between phytic acid and the plant proteins. Soybean and sesame protein form phytate complexes but corn germ does not.[699] The phytate band is visualized by

staining with ferric chloride, which produces a white precipitate on an orange background. A modified staining technique was found to be nonspecific.[815]

*(3) Mössbauer Spectroscopy*

Mössbauer spectroscopy of wheat seeds grown in a medium enriched in $^{57}Fe$ provides direct evidence that the iron in wheat is combined in the form of monoferric phytate in both seed and bran. Monoferric phytate exhibits a quadrupole splitting of 0.55 mm/s and an isomer shift of 0.77 mm/s relative to sodium nitroprusside at 80 K.[816] In soybean, however, the splitting is too large, suggesting some other combining form for the ferric ion. Ferrous ion is also present, especially in the immature seed.[817]

*(4) Fourier Transform Infrared (FTIR) Spectroscopy*

Sowa and Connor[818] used FTIR spectroscopy to follow the changes that occur in pine and spruce pollen during germination. The decrease in P—O vibrations in the 1300-900 $cm^{-1}$ frequency range reflects the utilization of phytate.

*(5) Light Microscopy*

The aleurone grains of barley and other plant seeds contain globoids that stain intensely red with toluidine blue owing to the presence of phytin.[819] This metachromasia, though not specific for phytin, is useful as an aid in the localization of phytin when used in conjunction with other methods. Another useful marker is acriflavine-HCl, which imparts an intense red fluorescence to phytin globoids.[820]

> *[Aleurone] layers were... fixed... in 2.5% glutaraldehyde in 0.05* M *cacodylate buffer, pH 7.2... for 6 h at 2 °C. After fixation, the layers were washed for 12-15 h in several changes of the fixing buffer at 2 °C. The tissue was supported in a gelatin-antifreeze medium... for sectioning at −24 °C... [2 μ] sections were stained in 0.02% toluidine blue O (Harleco, C.I. No. 52040) in acetate buffer... at pH 5.0. The slides were examined immediately after rinsing and mounting in buffer and also after dehydration in 95% ethanol (10 s), ethyl cellosolve (10 s) and xylene before mounting in Eukitt (O. Kindler, Freiburg).*
>
> Jacobsen, J. V.; Knox, R. R.; Pyliotis, N. A., "The Structure and Composition of Aleurone Grains in the Barley Aleurone Layer", *Planta* **1971**, *101*(3), 189–209,[819] reprinted by permission of Springer, © 1971.

*(6) Electron Microscopy*

Electron microscopy has been found to be useful in determining the distribution of phytic acid in plant tissues at the cellular level, particularly in plant species whose seeds contain phytin crystals embedded in protein bodies or globoids. The phytin crystals, which are naturally electron-dense, appear white in scanning electron microscopy (SEM) but black in transmission electron microscopy (TEM).[673b]

These techniques, in combination with X-ray microanalysis, also make it possible to determine the identity and relative amounts of mineral elements contained in phytin

globoids. Table 2-4 identifies studies in which electron microprobe X-ray (EMX) analysis has been used in combination with SEM and those in which energy-dispersive X-ray (EDX) analysis has been used in combination with either SEM or TEM.

> Scanning electron microscopy (SEM)—*Thick endosperm slices were fixed in half-strength Karnovsky's fixative (1965) in 50 mM phosphate buffer at pH 7.2 in the refrigerator for several days. Slices were rinsed in buffer, fractured with a dull razor blade and subsequently dehydrated in an acetone series. The tissue was critical point dried and the fractured surface was coated with a gold/palladium mixture. Specimens were viewed on a JEOL-35C microscope and photographed on Polaroid Type 55 film.*
>
> [Transmission] electron microscopy (TEM) and X-ray microprobe analysis (EDAX)—*Endosperm from seeds soaked for 2 to 7 days was cut into small pieces and fixed in 2 % glutaraldehyde in 50 mM phosphate buffer at pH 7.2 at room temperature for 4 to 6 hr and post-fixed in 1 % osmium tetroxide in the same buffer in the refrigerator overnight. The tissue was dehydrated in acetone and infiltrated in the low viscosity recipe of Spurrs' epoxy resin (Spurr, 1969) over several days. The blocks were sectioned on glass knives and stained with lead citrate and uranyl acetate. Specimens were viewed on a Phillips 400 electron microscope. For the EDAX preparations, tissue was fixed in 2 % glutaraldehyde in 50 mM cacodylate buffer and dehydrated in acetone without osmium post-fixation. Sections were collected on copper grids. Electron-opaque deposits were subjected to energy dispersive X-ray microanalysis using a Philips 400-EDAX 9100 system, an accelerating voltage of 40 or 60 KeV, and a takeoff angle of 24 degrees. A control spectrum was collected from an adjacent area of protein for each deposit analyzed.*
>
> DeMason, D. A., "Endosperm Structure and Storage Reserve Histochemistry in the Palm, *Washingtonia filifera*", *Am. J. Bot.* **1986**, *73*(9), 1332–1340,[1174] reprinted by permission of the Botanical Society of America, © 1986.

## Radioactive Labeling

Phytic acid labeled with $^{3}H$, $^{14}C$, or $^{32}P$ has been found to be useful in studies of the metabolism of phytic acid in birds, rats, and other animal species as well as in the plant itself. The radioisotope is usually introduced by incubating the seed with an aqueous solution of a labeled precursor such as [$^{3}H$]-*myo*-inositol, [$^{14}C$]-*myo*-inositol, or [$^{32}P$]-phosphoric acid, but it can also be injected into the stalks (Table 2-3).[1185,1190] In one study, the label was applied to plant cells in suspension culture.[1186]

## Other Inositol Isomers

L'Annunziata and Fuller[1080] isolated *myo*-, D-*chiro*-, and *muco*-inositol from the polyphosphates of ponderosa pine needles and velvet mesquite leaves recovered from forest or desert soils. It seems likely that these isomers are the result of epimerization of *myo*-inositol catalyzed by soil enzymes as they are not present in living ponderosa pine[818] or velvet mesquite[1094] tissue.

**Table 2-3** Radioactive Labeling

| No. | Plant | Plant part | References |
|---|---|---|---|
| Labeled with $^{3}H$ | | | |
| 2 | Rice | *Oryza sativa* L. | 1185,1186 |
| 8 | Wheat | *Triticum aestivum* L. | 811,1138,1185,1187 |
| 1 | Wheat, club | *Triticum compactum* L. | 1138 |
| Labeled with $^{14}C$ | | | |
| 1 | Water meal | *Wolffiella floridana* (Sm.) Thomps. | 695 |
| 1 | Gibbous duckweed | *Lemna gibba* L. | 695 |
| 1 | Mustard, white | *Sinapis alba* L. | 1188 |
| 1 | Rice | *Oryza sativa* L. | 1189 |
| 1 | Wheat | *Triticum aestivum* L. | 1190 |
| Labeled with $^{32}P$ | | | |
| 1 | Subclover | *Trifolium subterraneum* L. | 693 |
| 1 | Corn | *Zea mays* L. | 1191,1192 |
| 2 | Mung bean | *Vigna radiata* (L.) Wilcz. | 693,1193 |
| 2 | Rice | *Oryza sativa* L. | 783,1186,1187,1189 |
| 4 | Wheat | *Triticum aestivum* L. | 693,811,1187 |

**Table 2-4** Phytic Acid Content of Plants

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Abelmoschus esculentus* (L.) Moench (Okra) | | | | | |
| 1 | Vegetable | McCance | 0 | 0.616 | 821 |
| 1 | Boiled leaf | Harland | 0.129 | | 822 |
| *Abies nordmanniana* (Stev.) Spach. (Caucasian Fir) | | | | | |
| 1 | Pollen | PE | 0.04 | 0.56 | 788 |
| *Abutilon theophrasti* Medik. (Velvetleaf) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.84 | | 796 |
| *Acacia conferta* Cunn. ex Benth. (Crowded-Leaf Wattle) | | | | | |
| 1 | Seed cotyledon | TEM/EDX | + | | 823 |
| *Acacia decurrens* (Wendl.) Willd. (Green Wattle) | | | | | |
| 1 | Pollen | PE | 0 | 0.22 | 788 |
| *Acacia karoo* Hayne (Karroo Thorn) | | | | | |
| 1 | Seed, axis[a] | $^{31}P$ NMR | 86 | | 824 |
| 1 | –, cotyledon[a] | $^{31}P$ NMR | 79 | | 824 |
| *Acacia nilotica* (L.) Delile (Babul) | | | | | |
| 1 | Seed | McCance | 0.20 | 0.45 | 825 |
| *Acacia senegal* (L.) Willd. (Gum Arabic Tree) | | | | | |
| 1 | Seed | McCance | 0.29 | 0.48 | 825 |
| *Acer pseudoplatanus* L. (Sycamore Maple) | | | | | |
| 1 | Culture cells | $^{31}P$ NMR | + | | 51 |
| *Acer* spp. (Maple) | | | | | |
| 1 | Pea[b] | McCance | 0.194 | 0.334 | 826 |
| 1 | Fat-free leaf powder | Michel | Trace | | 757 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Achras zapota* L. (Chicle) | | | | | |
| 1 | Flesh | McCance | 0 | 0.051 | 827 |
| *Adansonia digitata* L. (Baobab) | | | | | |
| 1 | Seed | McCance | 0.106 | | 828 |
| 1 | Fruit pulp (milk) | Harland | 0.00011 | 0.0018 | 829 |
| *Adenanthera pavonina* L. (Coralwood) | | | | | |
| 1 | Seed | McCance | 0.17 | 0.49 | 825 |
| *Adonis turkestanicus* (Korsh.) (Adolf) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.79 | | 796 |
| *Aegilops speltoides* Tausch (Goatgrass) | | | | | |
| 1 | Seed | Harland | fig. | 0.710 | 830 |
| *Aesculus hippocastanum* L. (European Horse Chestnut) | | | | | |
| 1 | Fat-free leaf flour[b,c] | Michel | 0 | 0.0037 | 757 |
| *Afzelia africana* Sm. ex Pers. (African Mahogany) | | | | | |
| 1 | Seed | McCance | 0.23 | 0.39 | 825 |
| *Agropyron desertorum* (Fisch.) Schult. (Crested Wheatgrass) | | | | | |
| 1 | Seed | Harland | 0.27 | | 831 |
| 1 | Seed | Inositol | + | | 831 |
| *Albizia julibrissin* Durazz. (Mimosa) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.39 | | 795 |
| *Albizia lophantha* (Willd.) Benth. (Plume Albizzia) | | | | | |
| 1 | Seed, axis[a] | $^{31}$P NMR | 68 | | 824 |
| 1 | –, cotyledon[a] | $^{31}$P NMR | 75 | | 824 |
| *Alisma orientale* Juz. (Water Plantain) | | | | | |
| 1 | Rhizome | GFC | 0.098 | | 779 |
| 1 | Rhizome | Inositol, PC, PE, TLC | + | | 779 |
| *Allium ascalonicum* L. (Shallot) | | | | | |
| 1 | Root | McCance | 0.037 | 0.066 | 832 |
| *Allium cepa* L. (Onion) | | | | | |
| 1 | Leaf | McCance | 0.020 | 0.037 | 832 |
| 1 | Tuber | McCance | 0.006 | 0.031 | 832 |
| *Allium porrum* L. (Leek) | | | | | |
| 1 | Leaf | McCance | 0.004 | 0.032 | 832 |
| *Allium sativum* L. (Garlic) | | | | | |
| 1 | Leaf | McCance | 0.008 | 0.048 | 832 |
| 1 | Bulb | McCance | 0.064 | 0.196 | 832 |
| *Allium turcomanicum* Regel | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.96 | | 794 |
| *Alnus crispa* (Ait.) Pursh (Green Alder) | | | | | |
| 1 | Leaf and stem | McCance | negl.[d] | | 833 |
| *Aloe excelsa* A. Berger | | | | | |
| 1 | Pollen | PE | 0.03 | 0.31 | 788 |
| *Alternanthera sessilis* (L.) R. Br. (Siseles) | | | | | |
| 1 | Leaf | McCance | 0.027 | 0.063 | 832 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Althaea nudiflora* Lindl. | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.17 | | 796 |
| *Althaea officinalis* L. (Marsh Mallow) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.68 | | 796 |
| *Amaranthus caudatus* L. (Love-Lies-Bleeding) | | | | | |
| 4 | Seed | McCance | 0.37-0.52 | 0.46-0.62 | 834 |
| 1 | Seed[e] | Inositol | 0.42 | | 835 |
| 1 | Defatted seed meal | McCance | 0.39 | 0.71 | 836 |
| 1 | Leaf and stem | McCance | 0.043 | 0.290 | 837 |
| *Amaranthus cruentus* L. (Purple Amaranth) | | | | | |
| 4 | Whole grain | McCance | 0.15-0.16 | | 838 |
| 1 | –, dehulled | McCance | 0.14 | | 838 |
| 1 | –, hull | McCance | 0.14 | | 838 |
| 1 | Seed[e] | Inositol | 0.38 | | 835 |
| 1 | Defatted seed meal | McCance | 0.34-0.47 | 0.61-0.80 | 836 |
| *Amaranthus gracilis* Desf. (Spineless Amaranth) | | | | | |
| 1 | Whole seed[c] | MCance | 0.12 | | 839 |
| 1 | Leaf | McCance | 0.044 | 0.090 | 832 |
| *Amaranthus hybridus* L. (Smooth Pigweed) | | | | | |
| 1 | Whole grain | McCance | 0.17 | | 838 |
| *Amaranthus hypochondriacus* L. (Prince's Feather) | | | | | |
| 2 | Whole grain | McCance | 0.16-0.17 | | 838 |
| 1 | –, dehulled | McCance | 0.15 | | 838 |
| 1 | –, hull | McCance | 0.12 | | 838 |
| 1 | Seed[e] | Inositol | 0.42 | | 835 |
| 1 | Leaf[c] | McCance | 0.93 | 1.1 | 840 |
| *A. hybridus* × *A. hypochondriacus* | | | | | |
| 1 | Whole grain | McCance | 0.17 | | 838 |
| *Amaranthus mantegazzianus* | | | | | |
| 1 | Defatted seed meal | McCance | 0.38 | 0.77 | 836 |
| *Amaranthus polygamus* L. | | | | | |
| 1 | Whole seed[c] | McCance | 0.17 | | 839 |
| *Amaranthus retroflexus* L. (Redroot Pigweed) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.39 | | 796 |
| *Amaranthus spinosus* L. (Spiny Amaranth) | | | | | |
| 1 | Whole seed[c] | McCance | 0.15 | | 839 |
| *Amaranthus standleyanus* Parodi ex Cuvas (Indehiscent Pigweed) | | | | | |
| 1 | Seed flour | McCance | 0.29 | 0.57 | 841 |
| *Amaranthus tenuifolius* Willd. | | | | | |
| 1 | Whole seed[c] | McCance | 0.16 | | 839 |
| *Amaranthus thunbergii* Moq. (Wild Blite) | | | | | |
| 1 | Boiled leaf | Harland | 0.067 | | 822 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Amaranthus tricolor* L. (Tampala) | | | | | |
| 1 | Whole, except root and tough stem | McCance | 0.036 | 0.586 | 827 |
| 1 | Leaf[e] | | 0 | 0.024 | 842 |
| *Amorpha fruticosa* L. (Bastard Indigo) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.36 | | 795 |
| *Amorphophallus campanulatus* (Roxb.) Blume (Elephant Yam) | | | | | |
| 1 | Leaf | McCance | 0.008 | 0.048 | 832 |
| 1 | Tuber | McCance | 0.022 | 0.224 | 821 |
| *Anacardium occidentale* L. (Cashew) | | | | | |
| 1 | Nut | McCance | 0.170 | 0.574 | 842 |
| 1 | Seed cotyledon | TEM/EDX | + | | 843 |
| 1 | Young leaf | McCance | 0.067 | 0.122 | 832 |
| *Ananas comosus* (L.) Merr. (Pineapple) | | | | | |
| 1 | Peeled ripe fruit | McCance | 0.95 | | 844 |
| *Angelica acutiloba* Kitag. | | | | | |
| 1 | Root | GFC | 0.119 | | 779 |
| 1 | Root | Inositol, PC, PE, TLC | + | | 779 |
| *Annona muricata* L. (Soursop, Guayabano) | | | | | |
| 1 | Peeled ripe fruit | McCance | 1.28 | | 844 |
| *Annona squamosa* L. (Sweetsop, Ates) | | | | | |
| 1 | Peeled fruit | McCance | 0.80 | | 844 |
| *Antirrhinum majus* L. (Snapdragon) | | | | | |
| 1 | Pollen | PE | 0.59 | 1.55 | 788 |
| *Apium graveolens* L., var. *dulce* (Mill.) Pers. (Celery) | | | | | |
| 1 | Stalk | McCance | 0.006 | 0.031 | 832 |
| *Apium graveolens* L., var. *rapaceum* (Mill.) Gaud. (Celeriac) | | | | | |
| 1 | Stalk | McCance | 0.018 | 0.570 | 821 |
| *Arachis hypogaea* L. (Peanut) | | | | | |
| 9 | Seed | McCance | 0.289-0.396 | 0.46-0.54 | 845 |
| 6 | Seed, defatted flour | McCance | 0.395-0.623 | 0.616-0.969 | 846 |
| 1 | Seed, lipid-free cotyledon | McCance | 0.48 | 0.90 | 847 |
| 1 | –, protein-rich fraction | McCance | 0.14-1.60 | 0.32-1.87 | 847 |
| 1 | –, starch grain | McCance | 0.14 | 0.31 | 847 |
| 1 | –, cell wall | McCance | 0.003 | 0.09 | 847 |
| 1 | –, vascular tissue | McCance | 0.003 | 0.78 | 847 |
| 1 | Seed, protein isolate | McCance | ~0.28 | | 848 |
| 1 | Seed, aleurone grain[c] | McCance | 1.21 | 1.33 | 849 |
| 1 | –, globoid[c] | McCance | 7.88 | 7.4 | 849 |
| 1 | Nut | Harland | 0.279 | | 822 |
| 1 | Nut | PE | + | | 849 |
| 2 | Seed flour[b] | Harland | 0.412-0.546 | | 738 |
| 1 | Nut, defatted[b] | HPLC | 0.53 | | 850 |
| 1 | Seed, axis[a] | $^{31}$P NMR | 81 | | 824 |
| 1 | –, hypocotyl[a] | $^{31}$P NMR | 88 | | 824 |
| 1 | Seed, globoid[c] | Inositol | 7.22 | | 849 |
| 1 | Acid-washed fiber | Harland | 0.047 | | 851 |
| 1 | Leaf[f] | HPLC | 0.00013 | | 852 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Araucaria angustifolia* (Bert.) O. Kuntze (Paraná Pine) | | | | | |
| 1 | Defatted seed flour | McCance | 0.0588 | 0.303 | 853 |
| *Araucaria araucana* (Mol.) K. Koch (Monkey Puzzle Tree) | | | | | |
| 1 | Defatted seed meal | McCance | 0.0695 | 0.349 | 854 |
| *Araucaria bidwillii* Hook. Bunya Bunya | | | | | |
| 1 | Defatted seed flour | McCance | 0.0518 | 0.174 | 853 |
| 1 | Pollen | PE | 0.17 | 0.50 | 788 |
| *Arctotheca calendula* Wendl. | | | | | |
| 1 | Pollen | PE | 0 | 0.53 | 788 |
| *Arenga pinnata* (Wurmb) Merr. (Sugar Palm) | | | | | |
| 1 | Seed | McCance | 0.008 | 0.011 | 832 |
| *Artocarpus altilis* (Park.) Fosb. (Breadfruit) | | | | | |
| 1 | Fruit | McCance | 0.21 | | 844 |
| 1 | Peeled unripe fruit | McCance | 0.04 | 0.22 | 855 |
| *Artocarpus camansi* Blanco (Breadnut) | | | | | |
| 1 | Unripe fruit | McCance | 0.008 | 0.039 | 832 |
| *Artocarpus heterophyllus* Lam. (Jackfruit) | | | | | |
| 1 | Seed | McCance | 0.012 | 0.083 | 832 |
| 1 | Ripe fruit | McCance | 0.008 | 0.017 | 832 |
| 1 | Unripe fruit | McCance | 0.004 | 0.030 | 832 |
| *Astragalus bisulcatus* (Hook.) A. Gray (Milk Vetch) | | | | | |
| 1 | Seed embryo | TEM/EDX | + | | 856 |
| *Athyrium esculentum* (Rezt.) Copel. (Vegetable Fern) | | | | | |
| 1 | Leaf | McCance | 0.005 | 0.052 | 832 |
| *Atriplex patula* L. (Spreading Orach) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.51 | | 796 |
| *Avena nuda* L. (Naked Oats) | | | | | |
| 1 | Seed caryopsis | HPLC | + | | 857 |
| *Avena sativa* L. (Oats) | | | | | |
| 9 | Seed | McCance | 0.222-0.284 | 0.368-0.454 | 858 |
| 6 | Grain[b] | McCance | 0.13-0.29 | 0.19-0.44 | 859 |
| 5 | Whole grain | McCance | 0.54-0.87 | | 860 |
| 5 | –, groats | McCance | 0.72-1.12 | | 860 |
| 5 | –, hulls | McCance | 0.21-0.44 | | 860 |
| 6 | Threshed grain | McCance | 0.185-0.260 | 0.314-0.426 | 861 |
| 4 | Grain, groats | McCance | 0.29-0.39 | | 862 |
| 7 | Grain, groats | McCance | 0.27-0.40 | | 863 |
| 0 | Whole milled grain[b] | McCance | 0.185-0.227 | | 864 |
| 1 | Seed meal, pinhead[b] | McCance | 0.299 | 0.495 | 826 |
| 1 | Dehusked seed | McCance | 0.311-0.355 | 0.474-0.495 | 865 |
| 1 | –, meal | McCance | 0.291 | 0.507 | 865 |
| 1 | –, flakes | McCance | 0.183-0.226 | 0.325-0.367 | 865 |
| 1 | Grain, kernel | McCance | 0.20 | 0.34 | 866 |
| 1 | –, coarse bran | McCance | 0.28 | 0.15 | 866 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| 1 | –, fine bran | McCance | 0.34 | 0.10 | 866 |
| 1 | –, bran flour | McCance | 0.17 | 0.05 | 866 |
| 1 | –, white flour | McCance | 0.11 | 0.04 | 866 |
| 2 | Seed[b] | Harland | 0.263-0.347 | | 738 |
| 1 | Seed hull | Harland | 0.010 | | 851 |
| 1 | Entire panicle (early dough stage)[b] | Harland | 0.028 | 0.32 | 867 |
| 2 | Seed, aleurone tissue | Microscopy | + | | 868,869 |
| 1 | Seed, aleurone cell | SEM | + | | 870 |
| 1 | Seed aleurone protein body | Harland | 0.72 | 0.82 | 871 |
| 1 | Starchy seed endosperm | Harland | 0.00 | 0.69 | 871 |
| 1 | Seed embryo | TEM/EDX | + | | 872 |
| 1 | Acid-washed fiber | Harland | 0 | | 851 |
| 1 | Whole seed[b] | HPLC | 0.21 | | 774 |
| 1 | –, groats | HPLC | 0.38 | | 774 |
| 1 | –, bran | HPLC | 0.39 | | 774 |
| 1 | Seed kernel flour | $^{31}$P NMR | 0.369 | | 873 |
| 1 | Seed | Inositol | 0.264 | | 874 |
| 1 | Whole seed | Phytase | + | + | 14 |
| 1 | Defatted seed powder | Michel | 0.272 | | 758 |
| 1 | 10-day seedling | Inositol | 0.227 | | 874 |
| 1 | Shoot | Harland | 0 | | 875 |
| 1 | Root | Harland | 0 | | 875 |
| *Avena strigosa* Schreb. (Bristle Oats) | | | | | |
| 1 | Threshed grain | McCance | 0.233-0.308 | 0.395-0.483 | 861 |
| *A. strigosa* × *A. brevi* | | | | | |
| 1 | Threshed grain | McCance | 0.272-0.322 | 0.452-0.489 | 861 |
| *Averrhoa carambola* L. (Carambola) | | | | | |
| 1 | Fruit | McCance | 0.022 | 0.044 | 832 |
| *Azadirachta indica* A. Juss. (Neem) | | | | | |
| 1 | Seed | McCance | 0.098 | | 828 |
| 1 | Leaf | McCance | 0.89 | 0.4 | 840 |
| *Azolla africana* Desv. (Water Fern) | | | | | |
| 1 | Leaf protein concentrate | McCance | 0.169 | | 876 |
| 1 | –, pulp | McCance | 0.155 | | 876 |
| 1 | –, juice | McCance | 0.008 | | 876 |
| *Bambusa spinosa* Roxb. (Bamboo) | | | | | |
| 1 | Shoot | McCance | 0.002 | 0.026 | 832 |
| *Banksia coccinea* R.Br. (Scarlet Banksia) | | | | | |
| 1 | Seed cotyledon | Microscopy | + | | 877 |
| *Banksia hookeriana* Meissn. (Hooker's Banksia) | | | | | |
| 1 | Seed cotyledon | Microscopy | + | | 877 |
| 1 | Seed cotyledon | SEM/EMX | + | | 877 |
| *Basella rubra* L. (Malabar Nightshade) | | | | | |
| 1 | Leaf | McCance | 0.006 | 0.076 | 832 |
| *Bauhinia monandra* Kurz (Butterfly Flower) | | | | | |
| 1 | Seed | McCance | 0.25 | 0.41 | 825 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Bauhinia purpurea* L. (Purple Bauhinia) | | | | | |
| 1 | Seed | McCance | 0.135 | 0.365 | 878 |
| *Bauhinia variegata* L. (Orchid Tree) | | | | | |
| 1 | Seed axis[a] | $^{31}$P NMR | 79 | | 824 |
| 1 | –, hypocotyl[a] | $^{31}$P NMR | 91 | | 824 |
| *Benincasa hispida* (Thumb.) Cogn. (Wax Gourd) | | | | | |
| 1 | Gourd | McCance | 0.003 | 0.018 | 832 |
| *Berlinia auriculata* Benth. | | | | | |
| 1 | Seed | McCance | 0.12 | 0.18 | 825 |
| *Bertholletia excelsa* Humb. and Bonpl. (Brazil Nut) | | | | | |
| 1 | Nut | McCance | 0.313 | 0.805 | 842 |
| 1 | Radicle | TEM/EDX | + | | 879 |
| *Beta vulgaris* (L.) Banks (Sugar Beet) | | | | | |
| 1 | Leaf | Michel | 0.0048 | 0.091 | 15 |
| 1 | Root | Michel | 0.0029 | 0.057 | 15 |
| 1 | Tuber | McCance | 0.012 | 0.039 | 832 |
| 1 | Tuber[b] | HPLC | 0.003 | | 774 |
| 1 | Tuber | $^{31}$P NMR | n.d. | | 43 |
| 1 | Acid-washed fiber | Harland | 0.006 | | 851 |
| *Betula papyrifera* (Reg.) Fern and Raup (Paper Birch) | | | | | |
| 1 | Leaf and stem | McCance | negl.[d] | | 833 |
| *Bixa orellana* L. (Annatto) | | | | | |
| 1 | Seed | McCance | 0.094 | | 828 |
| *Blighia sapida* K. König (Akee) | | | | | |
| 1 | Seed | McCance | 0.290 | | 828 |
| *Brassica campestris* L. (Turnip Rape) | | | | | |
| 2 | Seed | McCance | 0.69-0.72 | | 880 |
| 4 | Defatted seed flour | McCance | 1.1-1.4 | | 881 |
| 1 | Defatted seed meal | Harland | 1.1 | | 882 |
| 1 | Defatted seed flour[b] | Harland | 1.63 | | 883 |
| 2 | Seed meal, defatted (1) | Phytase | 0.99-1.11 | 1.08-1.18 | 745 |
| | Seed meal, defatted (2) | Phytase | 0.74-0.85 | 1.08-1.18 | 745 |
| 3 | Seed tissue | Microscopy | + | | 820 |
| 1 | Seed embryo | TEM/EDX | + | | 884 |
| 1 | Leaf | McCance | 0.025 | | 885 |
| Turnip rape, low erucic acid (Canola) | | | | | |
| 57 | Seed | Phytase | 0.98-1.43 | | 745 |
| *Brassica carinata* A. Braun (Abyssinian Mustard) | | | | | |
| 2 | Seed | McCance | 0.52-0.62 | | 886 |
| 4 | Seed | McCance | 0.65-0.71 | | 880 |
| 4 | Defatted seed meal | McCance | 0.99-1.07 | | 880 |
| *Brassica chinensis* L. (Pak-choi) | | | | | |
| 1 | Leaf | McCance | 0.012 | 0.041 | 832 |
| 1 | Boiled leaf | Harland | 0.022 | | 822 |
| *Brassica integrifolia* (West) Rupr. (Indian Brown Mustard) | | | | | |
| 1 | Leaf | McCance | 0.017 | 0.022 | 832 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Brassica juncea* L. (Indian Mustard) | | | | | |
| 4 | Seed | McCance | 0.72-1.01 | | 880 |
| 4 | –, defatted meal | McCance | 0.99-1.07 | | 880 |
| 1 | Seed embryo | SEM, TEM/EDX | + | | 884 |
| 1 | Seed, protein isolate | McCance | 0.56 | | 887 |
| *Brassica napobrassica* (L.) Mill. (Rutabaga) | | | | | |
| 1 | Tuber[b,f] | McCance | 0 | 0.0190 | 735 |
| *Brassica napus* L. (Rape) | | | | | |
| 3 | Seed[c] | McCance | 0.85-1.21 | 1.04-1.49 | 751 |
| 3 | Seed meal, defatted | McCance | 0.82-1.04 | 1.14-1.34 | 745 |
| 3 | Seed meal, defatted | Phytase | 0.90-1.10 | 1.14-1.34 | 745 |
| 1 | Seed meal, defatted | HPLC | + | | 888 |
| 6 | Seed, defatted flour | McCance | 1.0-1.4 | | 881 |
| 1 | –, hull | McCance | 0.10 | | 881 |
| 2 | Defatted seed meal | Harland | 1.2-1.3 | | 882 |
| 1 | Seed flour | Harland | 0.828 | 1.507 | 889 |
| 1 | –, protein concentrate | Harland | 0.999 | 1.737 | 889 |
| 1 | Seed, protein concentrate | McCance | 1.534 | 1.737 | 889 |
| 1 | Seed, protein isolate | McCance | 0.004-0.011 | 0.23-1.14 | 890 |
| 1 | Seed, flour | Phytase | 0.860 | 1.507 | 889 |
| 1 | –, protein concentrate | Phytase | 1.078 | 1.737 | 889 |
| 2 | Seed tissue | Microscopy | + | | 820 |
| 1 | Seed embryo | TEM/EDX | + | | 884 |
| 1 | Root | SEM/EMX | + | | 891 |
| Rape, low erucic acid (Canola) | | | | | |
| 127 | Seed meal, defatted | Phytase | 0.90-1.62 | | 745 |
| Rape, low glucosinolate (Canola) | | | | | |
| 4 | Seed | Harland | 0.35-0.65 | | 886 |
| 4 | Defatted seed meal | McCance | 0.95-1.14 | 1.13-1.43 | 892 |
| 1 | Defatted seed meal | Harland | 0.98 | 1.25 | 892 |
| 1 | Seed, protein isolate | McCance | 0.01-0.02 | | 893 |
| Rape, low glucosinolate, low erucic acid (Canola) | | | | | |
| 19 | Defatted seed meal | Phytase | 1.09-1.45 | | 745 |
| 5 | Defatted seed meal[c] | McCance | 0.82-0.96 | 1.27-1.55 | 894 |
| 2 | Defatted seed meal | McCance | 0.82-0.90 | | 887 |
| 2 | –, protein isolate | McCance | 0.62-0.73 | | 887 |
| *Brassica oleracea* L. ssp. *acephala* (Collards) | | | | | |
| 1 | Leaf[f] | HPLC | 0.0011 | | 852 |
| *Brassica oleracea* L. ssp. *botrytis* L. (Cauliflower) | | | | | |
| 1 | Flower | McCance | 0.007 | 0.030 | 832 |
| *Brassica oleracea* L. ssp. *capitata* L. (Cabbage) | | | | | |
| 1 | Leaf | McCance | 0.011 | 0.499 | 821 |
| 1 | Leaf[f] | HPLC | 0.00028 | | 852 |
| 1 | Root | SEM/EMX | + | | 891 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Brassica oleracea* L. ssp. *gemmifera* Zenk. (Brussels Sprouts) | | | | | |
| 1 | Inner leaf | McCance | 0.037 | 0.630 | 827 |
| *Brassica oleracea* L. ssp. *italica* Plenck. (Broccoli) | | | | | |
| 1 | Sprout[b] | HPLC | 0 | | 741 |
| *Brassica rapa* L. (Turnip) | | | | | |
| 1 | Leaf[f] | HPLC | 0.00009 | | 852 |
| 1 | Tuber[b,f] | McCance | 0 | 0.0275 | 735 |
| *Bromus pratensis* Lam. (Brome Grass) | | | | | |
| 1 | Defatted seed powder | Michel | 0.218 | | 758 |
| *Buchanania latifolia* Roxb. (Chirauli Nut) | | | | | |
| 1 | Nut | McCance | 0.163 | 0.716 | 827 |
| *Bulnesia bonariensis* Griseb. (Jaboncillo) | | | | | |
| 1 | Seed cotyledon | TEM | + | | 895 |
| *Bulnesia schickendantzii* Hieron | | | | | |
| 1 | Seed cotyledon | TEM | + | | 895 |
| *Cajanus cajan* (L.) Huth (Pigeon Pea) | | | | | |
| 22 | Pea[c] | McCance | 0.8-2.0 | 0.230-0.350 | 896 |
| 10 | Pea | McCance | 0.00003-0.00011 | | 897 |
| 6 | Whole seed | McCance | 0.265 ± 0.020 | 0.390 ± 0.032 | 898 |
| 6 | –, decorticated | McCance | 0.267 ± 0.017 | 0.411 ± 0.029 | 898 |
| 18 | Decorticated seed | McCance | 0.184-0.476 | 0.292-0.560 | 899 |
| 1 | Pea | Harland | 0.194-0.222 | | 822 |
| 2 | Seed | HPLC | 0.035-0.038 | | 900 |
| 1 | Seed, axis[a] | $^{31}$P NMR | 43 | | 824 |
| 1 | –, cotyledon[a] | $^{31}$P NMR | 55 | | 824 |
| 1 | 3-day sprout | McCance | 0.043 | | 901 |
| *Calendula officinalis* L. (Pot Marigold) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.73 | | 794 |
| *Canarium ovatum* Engl. (Pili Nut) | | | | | |
| 1 | Nut | McCance | 0.097 | 0.555 | 832 |
| *Canavalia ensiformis* (L.) DC (Jack Bean) | | | | | |
| 1 | Bean | McCance | 0.156 | | 902 |
| 1 | Seed | HPLC | 0.033 | | 900 |
| *Cannabis sativa* L. (Hemp) | | | | | |
| 1 | Seed[b] | McCance | 0.285 | 0.692 | 826 |
| 1 | Decorticated seed[b,c] | Posternak | 1.330 | 1.460 | 807 |
| 1 | –, aleurone grain[b,c] | Posternak | 3.61 | 3.83 | 807 |
| *Capparis decidua* (Forsk.) Edgew. (Ker) | | | | | |
| 1 | Unripe fruit | McCance | 0.086 | 0.179 | 903 |
| *Capsella bursa-pastoris* (L.) Medik. (Shepherd's Purse) | | | | | |
| 1 | Seed embryo | TEM/EDX | + | | 904 |
| *Capsicum annuum* L. (Sweet Pepper) | | | | | |
| 1 | Pod | McCance | 0.080 | 0.386 | 821 |
| 1 | Fruit | McCance | 0.017 | 0.027 | 832 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Capsicum frutescens* L. (Chili Pepper) | | | | | |
| 1 | Leaf | McCance | 0.010 | 0.054 | 832 |
| *Carapa procera* DC (African Crabwood) | | | | | |
| 1 | Seed | McCance | 0.093 | | 828 |
| *Carduus acanthoides* L. (Black Thistle) | | | | | |
| 1 | Defatted seed flour | McCance | 0.097 | 0.955 | 905 |
| *Carica papaya* L. (Papaya) | | | | | |
| 1 | Young leaf | McCance | 0.019 | 0.100 | 832 |
| 1 | Unripe fruit | McCance | 0.005 | 0.030 | 832 |
| 1 | Peeled ripe fruit | McCance | 0.36 | | 844 |
| *Carpinus betulus* L. (European Hornbeam) | | | | | |
| 1 | Fat-free leaf powder[b,c] | Michel | Trace | | 757 |
| *Carthamus tinctorius* L. (Safflower) | | | | | |
| 1 | Seed, protein isolate[c] | McCance | 0.003 | 0.23 | 906 |
| *Carum copticum* (L.) Benth. and Hook. (Bishop's Weed) | | | | | |
| 1 | Seed | McCance | 0.332 | 0.346 | 821 |
| *Carya illinoinensis* (Wangenh.) K. Koch (Pecan) | | | | | |
| 2 | Nut[b,g] | McCance | 0.39-0.43 | | 907 |
| *Carya* spp. (Hickory) | | | | | |
| 2 | Nut | McCance | 0.42-0.47 | | 907 |
| *Cassia artemisiodes* DC (Silver Cassia) | | | | | |
| 1 | Seed cotyledon | TEM/EDX | + | | 823 |
| *Cassia nodosa* Buch.-Ham. ex Roxb. (Jointwood) | | | | | |
| 1 | Seed | McCance | 0.12 | 0.39 | 825 |
| *Cassia sericea* Sweet | | | | | |
| 1 | Seed | McCance | 0 | | 908 |
| *Cassia sieberiana* DC (African Laburnum, Ratu) | | | | | |
| 1 | Seed | McCance | 0.26 | 0.45 | 825 |
| *Castanea sativa* Mill. (Spanish Chestnut) | | | | | |
| 1 | Fat-free leaf powder[b,c] | Michel | Trace | | 757 |
| *Castanea* spp. (Chestnut) | | | | | |
| 1 | Nut[b,f] | McCance | 0.009 | 0.074 | 735 |
| *Casuarina cunninghamiana* Miq. (Cunningham Beefwood) | | | | | |
| 1 | Seed cotyledon | TEM/EDX | + | | 872 |
| *Casuarina littoralis* Salisb. (Black She Oak) | | | | | |
| 1 | Seed cotyledon | TEM/EDX | + | | 872 |
| *Casuarina muelleriana* Miq. (Slaty She Oak) | | | | | |
| 1 | Seed cotyledon | TEM/EDX | + | | 872 |
| *Cedrela odorata* L. (Spanish Cedar) | | | | | |
| 1 | Seed | McCance | 0.338 | | 828 |
| *Ceiba pentandra* (L.) Gaertn. (Kapok Tree) | | | | | |
| 1 | Seed meal | McCance | 0.64 | 0.93 | 855 |
| *Celosia argentea* L. (Cockscomb) | | | | | |
| 1 | Leaf | McCance | 0.151 | 1.2 | 909 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Centaurea calcitrapa* L. (Abrepuño Colorado (Star Thistle)) | | | | | |
| 1 | Defatted seed flour | McCance | 0.073 | 0.682 | 910 |
| *Centaurea solstitialis* L. (Abrepuño Amarillo (Yellow Star Thistle)) | | | | | |
| 1 | Defatted seed flour | McCance | 0.084 | 0.995 | 910 |
| *Ceratonia siliqua* L. (Carob) | | | | | |
| 1 | Seed, defatted flour | McCance | 0.14 | | 911 |
| 1 | –, protein isolate | McCance | 0.08 | | 911 |
| 1 | Seed germ | Harland | 0.55 | | 761 |
| 1 | Seed, axis[a] | $^{31}$P NMR | 92 | | 824 |
| 1 | –, cotyledon[a] | $^{31}$P NMR | 96 | | 824 |
| *Ceratophyllum* spp. (Hornwort) | | | | | |
| 1 | Whole plant | Harland | 0.0017 | 0.126 | 912 |
| *Chaenomeles japonica* Lindl. (Japanese Quince) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.39 | | 795 |
| *Chenopodium album* L. (Lambsquarters) | | | | | |
| 1 | Leaf | McCance | 0.084 | | 885 |
| *Chenopodium botrys* L. (Jerusalem Oak) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.11 | | 796 |
| *Chenopodium quinoa* Willd. (Quinoa) | | | | | |
| 5 | Grain | Undisclosed | 0.27-0.37 | | 913 |
| 1 | Whole seed | McCance | 0.174 | 0.360 | 914 |
| 1 | –, whole meal | McCance | 0.184 | | 914 |
| 1 | –, flour | McCance | 0.083 | | 914 |
| 1 | –, bran | McCance | 0.167 | | 914 |
| 1 | –, hulls | McCance | 0.077 | 0.320 | 914 |
| 1 | Seed | Harland | 0.293 | | 915 |
| 1 | –, polished | Harland | 0.220 | | 915 |
| 1 | Sweet, seed | HPLC | 0.206 | | 916 |
| 1 | Bitter, seed | HPLC | 0.160 | | 916 |
| *Chloris gayana* Kunth. (Rhodes Grass) | | | | | |
| 1 | Pollen | PE | 0 | 0.37 | 788 |
| *Chromolaena odorata* (L.) King and H. Rob. (Jack in the Bush) | | | | | |
| 1 | Leaf | McCance | 0.034 | 0.10 | 917 |
| *Chrysophyllum albidum* G. Don (African Starapple) | | | | | |
| 1 | Fruit, peel | McCance | 0.0002 | 0.077 | 918 |
| 1 | –, deseeded pulp | McCance | 0.0004 | 0.075 | 918 |
| *Cicer arietinum* L. (Chickpea) | | | | | |
| 11 | Seed | McCance | 0.25-0.31 | 0.286-0.338 | 919 |
| 8 | Whole seed | McCance | 0.211-0.225 | | 920 |
| 5 | Whole seed | McCance | 0.076-0.114 | 0.164-0.308 | 921 |
| 16 | Decorticated seed | McCance | 0.147-0.334 | 0.211-0.419 | 899 |
| 2 | Seed | HPLC | 0.107-0.110 | | 922 |
| 5 | Seed, cotyledon | McCance | 0.059-0.106 | 0.160-0.330 | 921 |
| 2 | Seed, dehulled | McCance | 0.27-0.37 | | 923 |
| 2 | –, hull | McCance | 0.02-0.056 | | 923 |
| 1 | Immature seed | McCance | 0-0.082 | 0.380-0.506 | 924 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| 1 | Pea | Harland | 0.095 | 0.257 | 925 |
| 1 | Defatted seed powder | Michel | 0.354 | | 758 |
| 1 | Defatted seed flour | Harland | 0.146 | | 926 |
| 1 | –, protein fraction | Harland | 0.360 | | 926 |
| 1 | –, starch fraction | Harland | 0.042 | | 926 |
| 1 | Seed, axis[a] | $^{31}$P NMR | 41 | | 824 |
| 1 | –, hypocotyl[a] | $^{31}$P NMR | 58 | | 824 |
| 8 | 68-h sprout | McCance | 0.147-0.153 | | 920 |
| 1 | Sprout | McCance | 0.035 | 0.230 | 927 |
| *Cichorium intybus* L. (Chicory) | | | | | |
| 1 | Seed flour | McCance | 0.048 | 0.536 | 928 |
| *Citrullus vulgaris* Schrad. (Watermelon) | | | | | |
| 1 | Seed | McCance | 0.600 | 1.456 | 929 |
| 1 | –, protein isolate | McCance | 0.28 | 0.30 | 930 |
| 1 | Defatted seed powder | Michel | 0.120 | | 758 |
| 1 | Fruit | McCance | 0.0017 | | 885 |
| *Citrus aurantium* L. (Sour Orange) | | | | | |
| 1 | Defatted seed powder | Michel | 0.2945 | | 758 |
| *Citrus limon* (L.) Burm. f. (Sour Lemon) | | | | | |
| 1 | Fruit[b] | McCance | 0.026 | | 931 |
| *Citrus nobilis* Lour. (Tangor) | | | | | |
| 1 | Defatted seed powder | Michel | 0.1162 | | 758 |
| *Citrus sinensis* (L.) Osbeck (Orange) | | | | | |
| 1 | Fruit[b] | McCance | 0.029 | | 931 |
| 1 | Acid-washed fiber | Harland | 0 | | 851 |
| *Clianthus formosus* (G. Don) Ford and Vick. (Sturt Desert Pea) | | | | | |
| 1 | Seed cotyledon | TEM/EDX | + | | 823 |
| *Clitoria ternatea* L. (Blue Pea) | | | | | |
| 1 | Leaf | McCance | 0.010 | 0.061 | 832 |
| *Cocos nucifera* L. (Coconut) | | | | | |
| 1 | Seed | McCance | 0.067 | 0.336 | 929 |
| 1 | Seed meal[b,c] | McCance | 0.258 | 0.505 | 932 |
| 1 | Nut[b,c] | Harland | 0.67 | | 933 |
| 1 | Shoot | McCance | 0.010 | 0.076 | 832 |
| *Coffea arabica* L. (Coffee) | | | | | |
| 5 | Bean | McCance | 0.062-0.098 | | 934 |
| 6 | Raw bean | HPLC | 0.046-0.104 | 0.159-0.214 | 935 |
| 1 | Roasted bean[b] | Harland | 0.050 | | 776 |
| *Cola acuminata* (Beauv.) Schott and Endl. (Abata Cola) | | | | | |
| 1 | Seed | McCance | 0.038 | 0.193 | 929 |
| *Colocasia antiquorum* Schott. (Egyptian Taro, Culcas) | | | | | |
| 1 | Stem and leaf | McCance | 0 | 0.562 | 827 |
| *Colocasia esculenta* (L.) Schott (Taro) | | | | | |
| 1 | Leaf | McCance | 0.009 | 0.042 | 832 |
| 1 | Root | McCance | 0.022 | 0.053 | 832 |
| 1 | Tuber[c] | Harland | 0.241 | | 936 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Conium maculatum* L. (Poison Hemlock) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.70 | | 796 |
| *Corchorus olitorius* L. (Tossa Jute) | | | | | |
| 1 | Leaf | McCance | 0.028 | 0.130 | 832 |
| *Coriandrum sativum* L. (Coriander) | | | | | |
| 1 | Seed | McCance | 0.350 | 0.454 | 821 |
| 1 | Leaf | McCance | 0.088 | 0.441 | 827 |
| *Corylus avellana* L. (European Hazel) | | | | | |
| 1 | Nut, shelled[b,e] | McCance | 0.099 | 0.230 | 937 |
| 1 | Nut, shelled | HPLC | 0.048 | 0.299 | 938 |
| 1 | Seed cotyledon | TEM/EDX | + | | 939 |
| *Coula edulis* Baill. (Gabon Nut) | | | | | |
| 1 | Seed | McCance | 0.211 | | 828 |
| *Crambe abyssinica* Hochst. (Crambe) | | | | | |
| 1 | Seed | SEM/EMX | + | | 940 |
| 1 | Seed | TEM/EDX | + | | 940 |
| *Crassocephalum biafrae* (Oliv. and Hiern) S. Moore (Sierra Leone Bologi) | | | | | |
| 1 | Leaf | McCance | 0.076 | 0.7 | 909 |
| *Crassocephalum crepidioides* (Benth.) S. Moore (Hawksbead Velvetplant) | | | | | |
| 1 | Leaf | McCance | 0.070 | 0.9 | 909 |
| *Cucumis melo* L. (Melon) | | | | | |
| 1 | Seed, protein isolate | McCance | 1.02 | 1.25 | 930 |
| 1 | Fruit | McCance | 0.004 | 0.011 | 832 |
| *Cucumis sativus* L. (Cucumber) | | | | | |
| 1 | Cotyledon | Microscopy | + | | 819 |
| 1 | –, aleurone grain | Microscopy | + | | 941 |
| 1 | Fruit | McCance | 0.026 | 0.036 | 832 |
| *Cucurbita andreana* Naudin. (Winter Squash) | | | | | |
| 1 | Seed cotyledon | TEM/EDX | + | | 942 |
| *Cucurbita digitata* Gray (Coyote Gourd) | | | | | |
| 1 | Defatted flour | McCance | 2.4 | | 943 |
| 1 | Defatted seed embryo | Harland | 0.87 | | 944 |
| *Cucurbita foetidissima* HBK (Calabazilla) | | | | | |
| 1 | Defatted flour | McCance | 2.2 | | 943 |
| 1 | Defatted seed embryo | Harland | 0.53 | | 944 |
| 1 | Seed cotyledon | TEM/EDX | + | | 942 |
| *Cucurbita maxima* Duch. (Hubbard Squash) | | | | | |
| 1 | Seed embryo, defatted | Harland | 0.31 | | 944 |
| 5 | Seed cotyledon | TEM/EDX | + | | 945,946 |
| 1 | Boiled leaf | Harland | | 0.087 | 822 |
| 1 | Young leaf | McCance | 0.003 | 0.046 | 832 |
| 1 | Fruit | McCance | 0.008 | 0.044 | 832 |
| 1 | Flower | McCance | 0.023 | 0.046 | 832 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Cucurbita mixta* Pang. (Silver-Seed Gourd) | | | | | |
| 1 | Seed cotyledon | TEM/EDX | + | | 942 |
| *Cucurbita moschata* (Duch.) Poir. (Warty Squash) | | | | | |
| 1 | Seed embryo, defatted | Harland | 0.56 | | 944 |
| 1 | Seed cotyledon | TEM/EDX | + | | 942 |
| *Cucurbita palmata* S. Wats. (Coyote Gourd) | | | | | |
| 1 | Defatted flour | McCance | 2.6 | | 943 |
| *Cucurbita pepo* L. (Pumpkin) | | | | | |
| 1 | Seed[b,c] | Harland | 1.21 | | 933 |
| 1 | Seed, unshelled | Lendle | 0.0031 | | 947 |
| 1 | Defatted seed embryo | Harland | 0.56 | | 944 |
| 1 | Seed cotyledon | TEM/EDX | + | | 942 |
| 1 | Defatted seed meal | McCance | 0.847 | 1.783 | 948 |
| 1 | –, protein concentrate | McCance | 1.016 | 1.853 | 948 |
| 1 | –, protein isolate | McCance | 0.158 | 0.766 | 948 |
| *Cuminum cyminum* L. (Cumin) | | | | | |
| 1 | Seed | McCance | 0.171 | 0.514 | 821 |
| *Curcuma longa* L. (Turmeric) | | | | | |
| 1 | Seed | McCance | 0.112 | 0.327 | 821 |
| *Cuscuta reflexa* Roxb. (Dodder) | | | | | |
| 1 | Stem | McCance | 0.0103 | 0.0198 | 814 |
| 1 | Stem | PC | + | 0.0198 | 814 |
| *Cyamopsis psoralioides* (Lam.) DC (Cluster Bean) | | | | | |
| 1 | Bean | McCance | 0.022 | 0.224 | 821 |
| *Cynoglossum creticum* Mill. (Blue Hound's Tongue) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.70 | | 795 |
| *Cyperus esculentus* L. (Yellow Nutsedge, Chufa) | | | | | |
| 1 | Defatted seed | McCance | 0.183 | 0.307 | 865 |
| 1 | Tuber | Harland | 0.204 | | 949 |
| *Cyphomandra betacea* (Cav.) Sendtn. (Tree Tomato) | | | | | |
| 1 | Flesh and seed | McCance | 0.043 | 0.333 | 827 |
| *Dactylis glomerata* L. (Orchard Grass) | | | | | |
| 1 | Defatted seed powder | Michel | 0.436 | | 758 |
| *Daniellia oliveri* Hutch. and Dalz. (African Copaiba Balsam) | | | | | |
| 1 | Seed | McCance | 0.13 | 0.19 | 825 |
| *Datura stramonium* L. (Jimsonweed) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.39 | | 796 |
| *Daucus carota* L. (Carrot) | | | | | |
| 1 | Tuber | McCance | 0 | 0.253 | 821 |
| 1 | Tuber[b] | HPLC | 0.145 | | 741 |
| 1 | Tuber[c] | PE | 0 | | 950 |
| 1 | Root | $^{31}$P NMR | n.d. | | 43 |
| *Delonix regia* (Boj.) Rafir. (Royal Poinciana, Flamboyant) | | | | | |
| 1 | Defatted seed flour[c] | McCance | 0.6 | | 951 |
| 1 | –, protein isolate | McCance | 0.03 | | 951 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Dendrobium lowii* Lindl. | | | | | |
| 1 | Pollen | PE | 0.04 | 0.56 | 776 |
| *Deschampsia caespitosa* (L.) Beauv. (Tufted Hairgrass) | | | | | |
| 1 | Root | SEM/EMX | + | | 952 |
| *Detarium microcarpum* Guill. and Perr. | | | | | |
| 1 | Seed | McCance | 0.06 | 0.56 | 825 |
| *Dioclea reflexa* Hook. f. (Sea Purse) | | | | | |
| 1 | Seed | McCance | 0.0896 | 0.420 | 953 |
| *Dioscorea alata* L. (Winged Yam) | | | | | |
| 6 | Tuber | McCance | 0.038 ± 0.013 | 0.171 ± 0.014 | 954 |
| 1 | Boiled root | Harland | 0.007 | | 955 |
| *Dioscorea batatas* Decne. (Chinese Yam) | | | | | |
| 1 | Tuber mucilage | PC, PE | + | 3-4 | 956 |
| *Dioscorea esculenta* (Lour.) Burk. (Lesser Yam) | | | | | |
| 3 | Tuber | McCance | 0.032 ± 0.003 | 0.117 ± 0.009 | 954 |
| *Dioscorea rotundata* Poir. (White Guinea Yam) | | | | | |
| 1 | Tuber | McCance | 0.055 | 0.092 | 929 |
| 1 | Tuber[b] | Harland | 0.179 | | 936 |
| *Dioscorea versicolor* Wall. | | | | | |
| 1 | Skinned tuber | McCance | 0.024 | 0.250 | 827 |
| *Dioscoreophyllum cumminsii* (Stapf.) Diels (Serendipity Berry) | | | | | |
| 1 | Seed | McCance | 0.248 | | 828 |
| *Diospyros discolor* Willd. (Persimmon) | | | | | |
| 1 | Peeled ripe fruit | McCance | 0.92 | | 844 |
| *Dipsacus fullonum* L. var. *sylvestris* (Teasel) | | | | | |
| 1 | Defatted seed flour | McCance | 0.148 | 1.376 | 957 |
| *Dipteryx alata* Vog. (Baru) | | | | | |
| 1 | Seed | | No data given in abstract | | 958 |
| *Diptychocarpus strictus* (Fisch.) Trautv. | | | | | |
| 1 | Defatted seed meal | McCance | 1.01 | 3.3 | 959 |
| *Dryandra formosa* Meissn. (Showy Dryandra) | | | | | |
| 1 | Seed cotyledon | Microscopy | + | | 877 |
| *Echinochloa frumentacea* Link. (Japanese Millet) | | | | | |
| 1 | Seed bran[c] | Suzuki | 0.344 | 0.765 | 797 |
| *Echium italicum* L. (Italian Bugloss) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.79 | | 795 |
| *Elaeis guineensis* Jacq. (Oil Palm) | | | | | |
| 1 | Seed meal | McCance | 0.481 | 0.576 | 932 |
| *Elaeocarpus oblongus* (Wild Olive) | | | | | |
| 1 | Fruit flesh and skin | McCance | 0.012 | 0.064 | 827 |
| *Eleocharis dulcis* (Burm. f.) Trin. (Water Chestnut) | | | | | |
| 1 | Nut | McCance | 0.067 | 0.146 | 832 |
| *Eleusine coracana* (L.) Gaertn. (Ragi) | | | | | |
| 12 | Colored seed[h] | McCance | 0.188 ± 0.0075 | 0.243 ± 0.0094 | 960 |
| 3 | White seed[h] | McCance | 0.154 ± 0.0060 | 0.214 ± 0.0020 | 960 |
| 1 | Seed flour | HPLC | 0.145 | 0.128 | 961 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Emilia sonchifolia* (L.) DC (Red Tasselflower) | | | | | |
| 1 | Leaf | McCance | 0.072 | 0.16 | 917 |
| *Enterolobium cyclocarpum* Griseb. (Elephant's Ear) | | | | | |
| 1 | Seed | McCance | 0.29 | 0.35 | 825 |
| *Erodium cicutarium* (L.) L'Hér. (Red-Stemmed Filaree) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.28 | | 796 |
| *Erythrina coralloides* DC (Naked Coral Tree) | | | | | |
| 1 | Seed, axis[a] | $^{31}$P NMR | 63 | | 824 |
| 1 | –, cotyledon[a] | $^{31}$P NMR | 79 | | 824 |
| *Eucalyptus deglupta* Bl. (Mindanao Gum) | | | | | |
| 1 | Seed | McCance | 0.275 | | 828 |
| *Eucalyptus erythrocorys* F. Muell. (Illyarie) | | | | | |
| 1 | Seed cotyledon | TEM/EDX | + | | 962 |
| *Eucalyptus youngiana* F. Muell. (Ooldea Mallee) | | | | | |
| 1 | Pollen | PE | 0.06 | 0.56 | 788 |
| *Euphorbia hirta* L. (Kaka Wie Adwe) | | | | | |
| 1 | Leaf | McCance | 0.184 | 0.004 | 963 |
| *Fagopyrum esculentum* Moench (Buckwheat) | | | | | |
| 1 | Dehusked grain | McCance | 0.322 | 0.410 | 827 |
| 1 | Seed, flour[b,g] | McCance | 0.52 | | 907 |
| 1 | –, hull[b,g] | McCance | 0.28 | | 907 |
| *Ferula karataviensis* (Regel and Schmalh.) Korov. | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.34 | | 794 |
| *Ferula kelleri* K.-Pol. | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 1.21 | | 794 |
| *Ficus carica* L. (Fig) | | | | | |
| 1 | Fruit[b] | McCance | 0.0119 | 0.0915 | 735 |
| *Foeniculum vulgare* Mill. (Fennel) | | | | | |
| 1 | Mature seed | McCance | 0.369 | | 964 |
| 1 | Immature seed | McCance | 0.328 | | 964 |
| *Fragaria* spp. (Strawberry) | | | | | |
| 1 | Fruit[b] | McCance | 0.010 | | 931 |
| *Fuchsia* spp. hort. (Fuchsia) | | | | | |
| 1 | Pollen | PE | 0.04 | 0.59 | 788 |
| *Garcinia kola* Heck. (Efiari) | | | | | |
| 1 | Fruit, mesocarp | McCance | 0.00025 | | 965 |
| 1 | –, pericarp | McCance | 0.00031 | | 965 |
| *Garcinia mangostana* L. (Mangosteen) | | | | | |
| 1 | Peeled ripe fruit | McCance | 0.19 | | 844 |
| *Gevuina avellana* Mol. (Chile Nut) | | | | | |
| 1 | Defatted meal | McCance | 0.157 | 0.419 | 966 |
| *Ginkgo biloba* L. (Ginkgo) | | | | | |
| 1 | Nut | Harland | 0.172 | | 967 |
| *Glaucium fimbrilligerum* Boiss. (Sea Poppy) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 2.25 | | 794 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Gleditsia triacanthos* L. (Honey Locust) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.62 | | 795 |
| 1 | Seed, axis[a] | $^{31}$P NMR | 82 | | 824 |
| 1 | –, hypocotyl[a] | $^{31}$P NMR | 90 | | 824 |
| *Glycine max* (L.) Merr. (Soybean) | | | | | |
| 38 | Seed | McCance | 0.391-0.648 | 0.58-0.91 | 968 |
| ~15 | Seed | McCance | 0.231-0.575 | 0.442-0.838 | 969 |
| 2 | Full-fat seed flour[b] | McCance | 0.424-0.509 | 0.563-0.676 | 970 |
| 7 | –, defatted[b] | McCance | 0.457-0.522 | 0.665-0.753 | 970 |
| 12 | Defatted seed meal | McCance | 0.16-0.20 | 0.73-0.86 | 971 |
| 7 | Bean[g] | McCance | 0.48-0.73 | | 907 |
| 15 | Seed | McCance | 0.282-0.414 | 0.532-0.745 | 858 |
| 5 | Bean | McCance | 0.42-0.53 | 0.341-0.410 | 919 |
| 17 | Defatted seed meal | Harland | 0.529-1.145 | 1.277-2.833 | 972 |
| 1 | Seed oil[b] | Harland | n.d. | | 973 |
| 1 | Seed bran | Harland | 0.029 | | 851 |
| 1 | Acid-washed fiber | Harland | 0.019 | | 851 |
| 4 | Bean | HPLC | 0.31-0.48 | | 765 |
| 1 | Seed | CZE | 0.771 | | 700 |
| 1 | Seed | Mössbauer | (–) | | 817 |
| 1 | Seed cotyledon | TEM/EDX | + | | 974 |
| 1 | Seed embryo axis | TEM/EDX | + | | 823 |
| 1 | Seed flake, defatted | DGE | + | | 699 |
| 1 | Flake, defatted[b] | HPLC | 0.50-0.52 | | 850 |
| 1 | Hull, defatted[b] | HPLC | 0.034 | | 850 |
| 1 | Seed, axis[a] | $^{31}$P NMR | 54 | | 824 |
| 1 | –, hypocotyl[a] | $^{31}$P NMR | 87 | | 824 |
| 1 | Seed protein isolate[b,c] | $^{31}$P NMR | 0.31 | | 781 |
| 1 | Seed meal[b] | Inositol | 0.581 | | 784 |
| 1 | Defatted seed flour[b] | Harland | 0.328 | | 926 |
| 1 | –, protein concentrate[b] | Harland | 0.381 | | 926 |
| 2 | Seed, protein concentrate[b] | McCance | 0.351-0.612 | 0.654-0.899 | 970 |
| 2 | Seed, protein isolate[b] | McCance | 0.56-0.58 | 0.847-0.885 | 975 |
| 1 | Seed, 7S protein | McCance | 0.39 | 0.63-0.68 | 976 |
| 1 | –, 11S protein | McCance | 0.02 | 0.08 | 976 |
| 1 | –, whey isolate | McCance | 12.77 | 10.49-15.20 | 976 |
| 2 | Seed protein isolate | Harland | 0.404-0.513 | | 738 |
| 1 | Seed protein isolate | DGE | + | | 815 |
| 1 | Seed protein isolate[b] | Harland | 0.20-0.69 | 0.38-0.84 | 977 |
| 1 | –, 7S protein | Harland | 0.15 | 0.61 | 977 |
| 1 | –, 11S protein | Harland | 0.007 | 0.060 | 977 |
| 3 | Protein isolate[b,c] | HPLC | 0.45-0.56 | 0.79-0.89 | 978 |
| 1 | –, 7S protein | HPLC | 0.02 | 0.18 | 978 |
| 1 | –, 11S protein | HPLC | 0.003 | 0.06 | 978 |
| 1 | Seed protein body | Harland | 0.53 | 0.78 | 979 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| 1 | –, globoid | Harland | 6.70 | 7.65 | 979 |
| 1 | Seed protein body[b] | Morton | 0.38 | 0.43 | 804 |
| 1 | Root | SEM/EMX | + | | 891 |
| 2 | 3-day sprout | McCance | 0.15-0.18 | 0.44-0.47 | 980 |
| 1 | 10-day seedling | Inositol | 0.464 | | 784 |
| 1 | Whole plant (early flowering stage)[b] | Harland | 0.009 | 0.28 | 867 |
| 1 | –, stem | Harland | 0.000 | 0.30 | 867 |
| 1 | –, young leaf | Harland | 0.000 | 0.41 | 867 |
| 1 | –, first trifoliate leaf | Harland | 0.014 | 0.28 | 867 |
| *Glycine soja* Sieb and Zucc. (Soybean) | | | | | |
| 20 | Seed<br>Several sources say *Glycine soja* is the same as *Glycine max*, but in this reference Raboy *et al.* provide data for 38 varieties of *G. max* and 20 varieties of *G. soja* | McCance | 0.529-0.780 | 0.81-1.07 | 968 |
| *Glycyrrhiza glabra* L. (Licorice) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.14 | | 795 |
| *Gnetum africanum* Wlew. (Afang) | | | | | |
| 1 | Leaf | McCance | 0.070 | 0.300 | 981 |
| *Gnetum buchholzianum* Engl. (Joint Fir) | | | | | |
| 1 | Leaf | McCance | 0.087 | 0.1 | 909 |
| *Gnetum gnemon* L. (Buko, Spinach Joint Fir) | | | | | |
| 1 | Leaf | McCance | 0.017 | 0.088 | 832 |
| *Gossypium barbadense* L. (Sea Island Cotton) | | | | | |
| 1 | Meal | McCance | 1.02 | | 982 |
| *Gossypium herbaceum* L. (Levant Cotton) | | | | | |
| 1 | Seed | McCance | 0.322-0.410 | | 865 |
| *Gossypium hirsutum* L. (Upland Cotton) | | | | | |
| 8 | Ground seed kernel | McCance | 0.429-1.069 | 0.692-1.315 | 983 |
| 8 | –, defatted | McCance | 0.686-1.768 | 1.078-2.200 | 983 |
| 3 | Acid-delinted seed | McCance | 0.649-0.958 | 0.796-1.148 | 984 |
| 1 | –, cotyledon | McCance | 0.046-0.654 | 0.716-1.361 | 984 |
| 1 | –, hypocotyl and root | McCance | 0.00 | 0.568-0.878 | 984 |
| 1 | Glandless defatted seed flour | McCance | 1.59 | 1.85 | 985 |
| 1 | Glandless seed, aleurone grain[c] | PE | 2.25 | 2.39 | 986 |
| 1 | –, globoid[c] | PE | 13.85 | 14.21 | 986 |
| 1 | –, globoid[c] | Inositol | 13.62 | 14.21 | 986 |
| *Gossypium* spp. (Cotton) | | | | | |
| 14 | Seed kernel, dehulled[c] | HPLC | 0.462-0.842 | | 685 |
| 14 | Seed kernel, dehulled[c] | Harland, near IR | | | 685 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| 1 | Seed protein fraction[b] | Fontaine | 1.151 | 1.164 | 802 |
| 1 | Cotyledon | Microscopy | + | | 819 |
| *Grevillea annulifera* F. Muell. (Prickly Plume Grevillea) | | | | | |
| 1 | Seed cotyledon | Microscopy | + | | 877 |
| 1 | Seed cotyledon | SEM/EMX | + | | 877 |
| *Grevillea leucopteris* Meissn. | | | | | |
| 1 | Seed cotyledon | Microscopy | + | | 877 |
| 1 | Seed cotyledon | SEM/EMX, TEM | + | | 877 |
| *Grewia asiatica* L. (Phalsa) | | | | | |
| 1 | Fruit, flesh, and skin | McCance | 0.068 | 0.203 | 827 |
| *Guizotia abyssinica* (L.f.) Cass. (Nigerseed) | | | | | |
| 1 | Lipid-protein seed concentrate | McCance | 0.835 | 2.75 | 987 |
| *Hakea platysperma* Hook. (Cricket Ball Hakea) | | | | | |
| 1 | Seed cotyledon | Microscopy | + | | 877 |
| 1 | Seed cotyledon | SEM/EMX, TEM | + | | 877 |
| *Hakea victoriae* J. Drumm. | | | | | |
| 1 | Seed cotyledon | Microscopy | + | | 877 |
| 1 | Seed cotyledon | SEM/EMX | + | | 877 |
| *Hedera helix* L. (English Ivy) | | | | | |
| 1 | Fat-free leaf powder[b,c] | Michel | Trace | | 757 |
| *Helianthus annuus* L. (Sunflower) | | | | | |
| 2 | Whole seed | McCance | 0.45-0.48 | | 988 |
| 1 | Mature seed | PC | + | | 810 |
| 1 | Whole seed[b,c] | McCance | 0.22 | | 989 |
| 1 | –, dehulled | McCance | 0.30 | | 989 |
| 1 | –, hull | McCance | 0.05 | | 989 |
| 1 | –, defatted flour | McCance | 0.54-0.56 | | 989 |
| 1 | –, protein isolate | McCance | 0.08-0.23 | | 989 |
| 1 | Whole seed | Harland | 0.43 | 0.53 | 990 |
| 1 | –, meal | Harland | 1.2 | 1.50 | 990 |
| 1 | –, kernel | Harland | 0.62 | 0.69 | 990 |
| 1 | –, hull | Harland | 0.03 | 0.04 | 990 |
| 1 | –, protein concentrate | Harland | 0.9 | 1.21 | 990 |
| 1 | Whole seed | HPLC | 0.48 | 0.53 | 990 |
| 1 | –, kernel | HPLC | 0.62 | 0.69 | 990 |
| 1 | –, hull | HPLC | 0 | 0.04 | 990 |
| 1 | –, meal | HPLC | 1.3 | 1.50 | 990 |
| 1 | –, protein concentrate | HPLC | 1.0 | 1.21 | 990 |
| 1 | Seed, cotyledon | TEM/EDX | + | | 843 |
| 1 | Seed protein isolate[b,c] | Harland | 0.28-1.04 | | 755 |
| 1 | Seed, protein concentrate | McCance | 0.94 | | 988 |
| 1 | Lipid-protein concentrate[c] | McCance | 0.880 | 1.67 | 987 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| 1 | Decorticated seed[b,c] | Posternak | 0.723 | 0.830 | 807 |
| 1 | –, aleurone grain[b,c] | Posternak | 2.71 | 2.78 | 807 |
| 1 | Germinated seed | $^{31}$P NMR | + | | 43 |
| 1 | Root | SEM/EMX | + | | 891 |
| 1 | Pollen | PE | 0 | 0.90 | 788 |
| *Helianthus tuberosus* L. (Jerusalem Artichoke) | | | | | |
| 1 | Tuber | $^{31}$P NMR | + | | 43 |
| 1 | Tuber, boiled[b,f] | McCance | 0.0092 | 0.0370 | 735 |
| 1 | Other parts | $^{31}$P NMR | 0 | | 45 |
| *Helichrysum bracteatum* (Vent.) Andr. (Golden Everlasting Daisy) | | | | | |
| 1 | Seed cotyledon | TEM/EDX | + | | 843 |
| *Heliotropium lasiocarpum* Fisch. and Mey. (Heliotrope) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.56 | | 794 |
| *Heliotropium olgae* Bunge | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.56 | | 795 |
| *Hevea brasiliensis* (Willd.) Müll. (Pará Rubber) | | | | | |
| 1 | Defatted seed kernel | McCance | 0.090 | 0.24 | 991 |
| 1 | Seed meal | McCance | 0.35 | 0.58 | 855 |
| *Hibiscus cannabinus* L. (Kenaf) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 1.3 | | 793 |
| *Hibiscus huegelii* Endl. (Lilac Hibiscus) | | | | | |
| 1 | Pollen | PE | 0.07 | 0.56 | 788 |
| *Hibiscus sabdariffa* L. (Roselle) | | | | | |
| 3 | Seed | McCance | 0.26-0.33 | | 992 |
| 1 | Leaf and stem | McCance | 0.004 | 0.228 | 837 |
| *Hippophae rhamnoides* L. (Sea Buckthorn) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.96 | | 796 |
| *Hordeum bulbosum* L. (Bulbous Barley) | | | | | |
| 1 | Pollen | PE | 0 | 0.40 | 788 |
| *Hordeum vulgare* L. (Barley) | | | | | |
| 18 | Seed | McCance | 0.273-0.327 | 0.397-0.494 | 858 |
| 9 | Seed | McCance | 0.27-0.31 | | 993 |
| 1 | Meal | McCance | 0.216 | 0.355 | 826 |
| 1 | High protein seed flour | McCance | 0.68-0.81 | | 765 |
| 1 | High bran seed flour | McCance | 0.90-0.98 | | 765 |
| 1 | Seed | Harland | 0.34 | | 994 |
| 3 | Seed, 2-rowed | Harland | 0.250-0.276 | | 995 |
| 3 | Seed, 6-rowed | Harland | 0.267-0.273 | | 995 |
| 1 | Seed[b] | HPLC | 0.33 | | 774 |
| 1 | Seed[b] | Inositol | 0.314 | | 784 |
| 1 | Seed | Michel | 0.143 | 0.253 | 996 |
| 2 | Seed aleurone tissue | Microscopy | + | | 819,868 |
| 2 | Seed aleurone cell | SEM/EDX | + | | 870 |
| 1 | Seed aleurone cell | TEM/EDX | + | | 870 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| 1 | Grain | CZE | 0.250 | | 746 |
| 1 | Seed bran[b,c] | Suzuki | 0.238 | 0.541 | 797 |
| 1 | Acid-washed fiber | Harland | 0.127 | | 851 |
| 1 | Defatted seed powder | Michel | 0.338 | | 758 |
| 1 | Germinated seed | HPLC | + | | 857 |
| 1 | 84-h sprout | McCance | 0.058 | 0.56 | 997 |
| *Hyoscyamus niger* L. (Henbane) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 1.01 | | 796 |
| *Hyphaene thebaica* (L.) Mart. (Doum Palm) | | | | | |
| 1 | Seed | McCance | 0.093 | | 828 |
| *Icacina manni* (Efik Isun) | | | | | |
| 1 | Peeled tuber | McCance | 0.042 | | 998 |
| *Ipomoea aquatica* Forssk. (Swamp Cabbage) | | | | | |
| 1 | Leaf | McCance | 0.010 | 0.058 | 832 |
| 1 | Stalk | McCance | 0 | 0.398 | 821 |
| *Ipomoea asarifolia* (Desr.) Roem. and Schult. (Ginger-Leaf Morning-Glory) | | | | | |
| 1 | Leaf | McCance | 0.025 | 0.13 | 917 |
| *Ipomoea batatas* (L.) Lam. (Sweet Potato) | | | | | |
| 1 | Young leaf | McCance | 0.019 | 0.068 | 832 |
| 1 | Leaf[f] | HPLC | 0.00059 | | 852 |
| 49 | Whole tuber, milled | McCance | 0.0014-0.0043 | 0.038-0.182 | 999 |
| 1 | Boiled tuber | Harland | 0.011 | | 822 |
| *Ipomoea involucrata* Beauv. (Iehowa Dua) | | | | | |
| 1 | Leaf | McCance | 0.050 | 0.034 | 963 |
| *Isoetes muelleri* A. Braun | | | | | |
| 1 | Corm | Microscopy | + | | 1000 |
| 1 | Corm | SEM, TEM | + | | 1000 |
| *Jatropha curcas* L. (Barbados Nut) | | | | | |
| 18 | Seed kernel | McCance | 1.85-2.84 | | 1001 |
| *Jatropha dulcis* J. F. Gmel. | | | | | |
| 1 | Root[b,c] | Undisclosed | + | | 1002 |
| *Jatropha utilissima* | | | | | |
| 1 | Root[b,c] | Undisclosed | + | | 1002 |
| *Juglans nigra* L. (Black Walnut) | | | | | |
| 1 | Nut[b,g] | McCance | 0.57 | | 907 |
| 1 | Pollen | PE | 0.22 | 0.46 | 788 |
| *Juglans regia* L. (English Walnut) | | | | | |
| 1 | Nut | McCance | 0.179 | 0.403 | 842 |
| 1 | Seed cotyledon | TEM/EDX | + | | 939 |
| *Kerstingiella geocarpa* Harms. (Kersting's Groundnut) | | | | | |
| 1 | Seed | | 0.014-0.084 | | 1003 |
| *Lablab purpureus* (L.) Sweet (Hyacinth Bean) | | | | | |
| 5 | Seed | | 0.282-0.380 | 0.385-0.483 | 1004 |
| 1 | Seed, axis[a] | $^{31}$P NMR | 67 | | 824 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| 1 | Seed, hypocotyl[a] | $^{31}$P NMR | 74 | | 824 |
| 1 | Boiled bean | Harland | 0.070 | | 822 |
| *Lactuca sativa* L. (Lettuce) | | | | | |
| 1 | Seed | McCance | 0.39 | | 1005 |
| 1 | –, cotyledon | McCance | 0.31 | | 1005 |
| 1 | –, axis | McCannce | 0.08 | | 1005 |
| 1 | –, endosperm | McCance | 0.007 | | 1005 |
| 1 | Leaf[b] | HPLC | 0 | | 741 |
| 1 | Leaf[c] | $^{31}$P NMR | + | | 48 |
| *Lagenaria siceraria* (Mol.) Standl. (Bottle Gourd) | | | | | |
| 1 | Gourd | McCance | 0.003 | 0.017 | 832 |
| *Lansium domesticum* Corr. Serr. (Lansones, Langsat) | | | | | |
| 1 | Peeled ripe fruit | McCance | 0.31 | | 844 |
| *Larix laricina* (Du Roi) K. Koch (American Larch) | | | | | |
| 1 | Needle and seed | McCance | negl.[d] | | 833 |
| *Lasianthera africana* P.B. Mundja (Editan) | | | | | |
| 1 | Leaf | McCance | 0.038 | 0.425 | 981 |
| *Lathyrus sativus* L. (Grass Pea) | | | | | |
| 1 | Seed | McCance | 0.082 | 0.262 | 827 |
| 1 | Seed | Harland | 0.325 | | 1006 |
| *Lathyrus tingitanus* L. (Tangier Pea) | | | | | |
| 2 | Seed | McCance | 0.13-0.15 | 0.32-0.35 | 859 |
| *Launaea taraxacifolia* (Willd.) Amin (Wild Lettuce) | | | | | |
| 1 | Leaf | McCance | 2.61 [*sic*] | 0.012 | 963 |
| *Lemna gibba* L. (Gibbous Duckweed) | | | | | |
| 1 | Whole plant | PE | + | | 695 |
| *Lemna minor* L. (Lesser Duckweed) | | | | | |
| 1 | Whole plant | GFC | + | | 683 |
| 1 | Frond | SEM/EMX | + | | 1007 |
| 1 | Frond | TEM | + | | 1007 |
| *Lemna* spp. (Duckweed) | | | | | |
| 1 | Whole plant | Harland | 0.0069 | 0.384 | 912 |
| *Lens culinaris* Medic. (Lentil) | | | | | |
| ~15 | Seed | McCance | 0.044-0.339 | 0.234-0.544 | 969 |
| 2 | Seed | McCance | 0.120-0.195 | 0.153-0.247 | 1008 |
| 4 | Seed | McCance | 0.043-0.051 | 0.261-0.331 | 1009 |
| 5 | Seed | McCance | 0.08-0.11 | 0.190-0.217 | 919 |
| 3 | Seed | Harland | 0.236-0.295 | | 1006 |
| 2 | Seed | Harland | 0.042-0.434 | 0.23-0.67 | 1010 |
| 1 | Seed | HPLC | 0.069 | | 922 |
| 1 | Defatted seed powder | Michel | 0.3685 | | 758 |
| 1 | Flour | Harland | 0.180 | | 926 |
| 1 | –, protein fraction | Harland | 0.528 | | 926 |
| 1 | –, starch fraction | Harland | 0.042 | | 926 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Lepidium sativum* L. (Garden Cress) | | | | | |
| 1 | Seed | McCance | 0.457 | 0.747 | 827 |
| *Leucaena leucocephala* (Lam.) De Wit (Ipil Ipil (Leadtree)) | | | | | |
| 2 | Whole seed | McCance | 0.40-0.61 | 0.298-0.300 | 1011 |
| 2 | –, kernel | McCance | 0.42-0.73 | 0.607-0.615 | 1011 |
| 2 | –, hull | McCance | 0.33-0.35 | 0.052-0.054 | 1011 |
| 1 | Seed, axis[a] | $^{31}$P NMR | 78 | | 824 |
| 1 | –, hypocotyl[a] | $^{31}$P NMR | 79 | | 824 |
| 1 | Leaf meal | McCance | 0.02 | 0.22 | 855 |
| *Lilium henryi* Bak. (Lily) | | | | | |
| 1 | Pollen | PE | 0.31 | 0.84 | 788 |
| *Lilium longiflorum* Thunb. (Trumpet Lily) | | | | | |
| 1 | Pollen | McCance | 0.229 | 0.889 | 1012 |
| 1 | Pollen | Harland | 0.244 | 0.889 | 1012 |
| *Lindelofia macrostyla* (Bunge) M. Pop. | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.39 | | 794 |
| *Lindelofia tschimganica* (Lipsky) Pazij. | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.45 | | 794 |
| *Linum usitatissimum* L. (Flax) | | | | | |
| 1 | Whole seed, defatted | McCance | 0.606-0.785 | 0.818-1.077 | 865 |
| 1 | –, meal | McCance | 1.351 | 1.907 | 865 |
| 1 | –, shell | McCance | 0.270 | 0.350 | 865 |
| 1 | Defatted flour[b,c] | McCance | 1.7-1.8 | | 943 |
| 8 | Defatted meal | McCance | 0.374-1.071 | | 335 |
| 10 | Defatted meal | Harland | 0.68-0.76 | 0.99-1.07 | 1013 |
| 10 | Seed, protein isolate[i] | McCance | 0.36 | 0.45 | 1014 |
| 1 | Aleurone grain | Microscopy | + | | 941 |
| *Lolium cuneatum* Nevski (Poison Ryegrass) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.45 | | 794 |
| *Lolium multiflorum* Lam. (Italian Ryegrass) | | | | | |
| 1 | Root | SEM/EMX | + | | 891 |
| *Lolium* spp. (Ryegrass) | | | | | |
| 3 | Seed[b] | McCance | 0.19-0.27 | 0.35-0.43 | 1015 |
| *Lonicera nummulariifolia* Jaub. and Spach. (Honeysuckle) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.42 | | 796 |
| *Lophira alata* Banks (Niam Tree) | | | | | |
| 1 | Seed | McCance | 0.204 | | 828 |
| *Lotus corniculatus* L. (Birdsfoot Trefoil) | | | | | |
| 1 | Root | McCance | 0.023 | 0.55 | 1016 |
| *Luffa acutangula* (L.) Roxb. (Angled Luffa) | | | | | |
| 1 | Gourd[e] | McCance | 0 | 0.037 | 842 |
| *Luffa aegyptiaca* Mill. (Sponge Gourd) | | | | | |
| 1 | Gourd | McCance | 0.009 | 0.031 | 832 |
| 1 | Seed, protein isolate | McCance | 0.40 | 0.47 | 930 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Lupinus albus* L. (White Lupine) | | | | | |
| 4 | Seed[c] | McCance | 0.40 ± 0.18 | | 1017 |
| 2 | Seed | McCance | 0.085-0.099 | 0.302-0.378 | 1018 |
| 2 | Seed | Harland | 0.14-0.17 | | 1019 |
| 1 | Seed | HPLC | 0.0087 | | 1020 |
| 1 | Seed flour | Harland | 0.230 | | 926 |
| 1 | Seed, axis[a] | $^{31}$P NMR | 0.630 | 0.714 | 824 |
| 1 | –, cotyledon[a] | $^{31}$P NMR | 0.309 | 0.334 | 824 |
| *Lupinus angustifolius* L. (Blue Lupine) | | | | | |
| 4 | Seed[c] | McCance | 0.41 ± 0.12 | | 1017 |
| 6 | Seed | Harland | 0.20-0.31 | | 1019 |
| 1 | Dehulled seed | McCance | 0.132 | 0.29 | 1021 |
| 1 | 6-day sprout | McCance | 0.045 | 0.35 | 1021 |
| *Lupinus atlanticus* Gladst. | | | | | |
| 2 | Seed | Harland | 0.31-0.34 | | 1019 |
| *Lupinus cosentinii* Guss. | | | | | |
| 1 | Seed | Harland | 0.11-0.17 | | 1019 |
| *Lupinus digitatus* Forsk. | | | | | |
| 1 | Seed | Harland | 0.22 | | 1019 |
| *Lupinus hispanicus* Boiss. and Reut. (Spanish Lupine) | | | | | |
| 1 | Seed | Harland | 0.34 | | 1019 |
| *Lupinus hispanicus* ssp. *bicolor* (Merino) Gladst. | | | | | |
| 18 | Seed[c] | McCance | 0.40 ± 0.07 | | 1017 |
| *Lupinus hispanicus* ssp. *hispanicus* | | | | | |
| 16 | Seed[c] | McCance | 0.42 ± 0.09 | | 1017 |
| *Lupinus luteus* L. (Yellow Lupine) | | | | | |
| 4 | Seed[c] | McCance | 0.76 ± 0.27 | | 1017 |
| 2 | Whole seed flour | Harland | 0.85-0.87 | | 1022 |
| 1 | Seed | HPLC | 0.201 | | 1020 |
| 1 | Seed aleurone grain | McCance | 1.07 | | 1023 |
| 1 | –, light | McCance | 0.53 | | 1024 |
| 1 | –, heavy | McCance | 3.58 | | 1024 |
| *Lupinus micranthus* Guss. | | | | | |
| 1 | Seed | Harland | 0.25 | | 1019 |
| *Lupinus mutabilis* Sweet (Tarwi) | | | | | |
| 4 | Seed[c] | McCance | 0.77 ± 0.10 | | 1017 |
| 1 | Seed axis[a] | $^{31}$P NMR | 78 | | 824 |
| 1 | –, cotyledon[a] | $^{31}$P NMR | 81 | | 824 |
| *Lupinus palestinus* Boiss. | | | | | |
| 1 | Seed | Harland | 0.34 | | 1019 |
| *Lupinus pilosus* L. (Blue Lupine) | | | | | |
| 2 | Seed | McCance | Trace-0.13 | 0.26-0.39 | 859 |
| 3 | Seed | Harland | 0.22-0.25 | | 1019 |
| *Lupinus polyphyllus* Lindl. (Washington Lupine) | | | | | |
| 1 | Seed | Harland | 0.20 | | 1019 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Lupinus* spp. (Lupine) | | | | | |
| 1 | Root | SEM/EMX | + | | 891 |
| *Lycopersicon esculentum* Mill. (Tomato) | | | | | |
| 1 | Seed | SEM | + | | 1025 |
| 1 | Seed cotyledon | TEM/EDX | + | | 1025 |
| 1 | Seed, defatted groats | McCance | 0.1-0.4 | | 1026 |
| 1 | Acid-washed fiber | Harland | 0.240 | | 851 |
| 1 | Root | SEM/EMX | + | | 891 |
| 1 | Whole plant[f] | McCance | 5.0 | | 1027 |
| 1 | Fruit | McCance | 0.010 | 0.021 | 832 |
| –, ssp. *cerasiforme* Alef. (Cherry Tomato) | | | | | |
| 1 | Seed | TEM/EDX | + | | 904 |
| *Lysiloma watsonii* Rose (Feathertree) | | | | | |
| 1 | Seed | Harland | 0.28 | | 1028 |
| *Macadamia integrifolia* Maid. and Bet. (Macadamia Nut) | | | | | |
| 1 | Seed cotyledon | TEM/EDX | + | | 939 |
| *Macrotyloma uniflorum* (Lam.) Verdc. (Horse Gram) | | | | | |
| 1 | Seed | McCance | 0.184 | 0.320 | 1029 |
| *Malus domestica* Borkh. (Apple) | | | | | |
| 1 | Stem cortex, 1 year old | McCance | 0.034 | | 1030 |
| 1 | Acid-washed fiber | Harland | 0.038 | | 851 |
| *Malus sylvestris* (L.) Mill. (Crabapple) | | | | | |
| 1 | Cored fruit | McCance | 0 | 0.129 | 827 |
| *Mangifera indica* L. (Mango) | | | | | |
| 1 | Seed kernel meal | McCance | 0.082 | 0.168 | 1031 |
| 2 | Fruit | McCance | 0.010-0.015 | 0.016-0.029 | 832 |
| 1 | Fruit | Harland | 0.039 | | 822 |
| *Manihot esculenta* Crantz (Cassava) | | | | | |
| 1 | Leaf, very young | McCance | 0.028 | 0.23 | 1032 |
| 1 | –, mature | McCance | 0.047 | 0.18 | 1032 |
| 1 | Leaf meal | McCance | 0.04 | 0.42 | 855 |
| 1 | Boiled leaf | Harland | 0.053 | | 822 |
| 1 | Tuber | McCance | 0.019 | 0.080 | 827 |
| 7 | Peeled tuber, edible portion | McCance | 0.26-0.56 | | 844 |
| 1 | Tuber flour | McCance | 0.0033 | 0.0327 | 1033 |
| 1 | Root | Harland | 0.045 | | 822 |
| *Maranta arundinacea* L. (Arrowroot) | | | | | |
| 1 | Root flour | McCance | 0 | 0.020 | 821 |
| *Marsdenia latifolium* Benth. (Utasi) | | | | | |
| 1 | Leaf | McCance | 0.031 | 0.395 | 981 |
| *Matricaria chamomilla* L. (Sweet False Chamomile) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.11 | | 794 |
| *Medicago sativa* L. (Alfalfa) | | | | | |
| 1 | Defatted seed[b] | McCance | 0.006 | 0.283 | 1034 |
| 1 | Seed meal[b] | McCance | 0.027 | 0.131 | 826 |
| 1 | Leaf protein concentrate | McCance | 0.00 | | 1035 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| 1 | Root | McCance | 0.009 | 0.43 | 1016 |
| 1 | Root | SEM/EMX | + | | 891 |
| 8 | Root and crown | McCance | 0.022-0.029 | 0.191-0.254 | 1036 |
| 3 | Root and crown | Harland | 0.006-0.016 | 0.191-0.221 | 1036 |
| 3 | Root and crown | PE | + | 0.191-0.221 | 1036 |
| 1 | Whole plant (1/4 bloom)[b] | Harland | 0.006 | 0.31 | 867 |
| *Melia azedarach* L. (Chinaberry) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.34 | | 796 |
| *Melilotus officinalis* (L.) Lam. (Yellow Sweet Clover) | | | | | |
| 1 | Root | McCance | 0.018 | 0.52 | 1016 |
| *Mentha spicata* L. (Spearmint) | | | | | |
| 1 | Leaf | McCance | 0.022 | 0.268 | 821 |
| *Metroxylon sagu* Rottb. (Sago Palm) | | | | | |
| 1 | Palm | McCance | 0 | 0.007 | 821 |
| 1 | Pith starch[b,f] | McCance | 0.019 | 0.038 | 735 |
| *Momordica charantia* L. (Balsam Pear) | | | | | |
| 1 | Leaf | McCance | 0.042 | 0.108 | 832 |
| 1 | Fruit | McCance | 0.004 | 0.050 | 832 |
| *Monodora ternifolia* | | | | | |
| 1 | Seed | McCance | 0.183 | | 828 |
| *Moringa oleifera* Lam. (Horseradish Tree) | | | | | |
| 1 | Leaf | McCance | 0.009 | 0.192 | 832 |
| 1 | Pod | McCance | 0.026 | 0.048 | 832 |
| *Moringa peregrina* (Forssk) Fion (Yassar) | | | | | |
| 1 | Seed, defatted flour | McCance | 0.732 | | 1037 |
| 1 | –, protein concentrate | McCance | 1.188 | | 1037 |
| 1 | –, protein isolate | McCance | 0.278 | | 1037 |
| *Mucuna deeringiana* (Bort.) Merr. (Velvet Bean) | | | | | |
| 1 | Bean | McCance | 0.17 | 0.29 | 855 |
| *Mucuna monosperma* DC ex Wight (Negro Bean) | | | | | |
| 2 | Bean | McCance | 0.142-0.178 | | 1038 |
| *Mucuna utilis* (Wight) Burck. (Mucuna Bean) | | | | | |
| 1 | Whole seed | McCance | 0.087 | 0.22 | 1039 |
| *Murraya koenigii* (L.) Spreng. (Curry Leaf) | | | | | |
| 1 | Leaf | McCance | 0.010 | 0.170 | 821 |
| *Musa errans* (Blanco) T.B. Teodoro (Botoan) | | | | | |
| 1 | Inflorescence | McCance | 0.004 | 0.038 | 832 |
| *Musa* × *paradisiaca* L. (Banana) | | | | | |
| 4 | Fruit | McCance | 0.008-0.029 | 0.012-0.071 | 832 |
| 1 | Fruit | Harland | 0.022 | | 822 |
| 2 | Boiled ripe fruit | Harland | 0 | | 955 |
| 2 | Boiled unripe fruit | Harland | 0.0003-0.010 | | 955 |
| *Myriophyllum* spp. (Milfoil) | | | | | |
| 1 | Whole plant | Harland | 0.0058 | 0.149 | 912 |
| *Myristica fragrans* Houtt. (Nutmeg) | | | | | |
| 1 | Seed | McCance | 0.189 | 0.308 | 821 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Nasturtium officinale* R. Br. (Watercress) | | | | | |
| 1 | Leaf | McCance | 0.016 | 0.057 | 832 |
| *Nelumbo* spp. (Lotus) | | | | | |
| 1 | Stem[b] | McCance | 0 | 0.141 | 827 |
| 1 | Fruit | PE | + | | 779 |
| *Nitraria komarovii* Iljin and Lava | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.22 | | 794 |
| *Nitraria schoberi* L. | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.36 | | 794 |
| *Ocimum basilicum* L. (Basil) | | | | | |
| 1 | Leaf | McCance | 0.073 | 0.503 | 981 |
| *Ocimum viride* Willd. (Iko) | | | | | |
| 1 | Leaf | McCance | 0.025 | 0.440 | 981 |
| *Oenothera striata* Link. | | | | | |
| 1 | Pollen | PE | 0.11 | 0.40 | 788 |
| *Onopordon acanthium* L. (Scotch Thistle) | | | | | |
| 1 | Defatted flour | McCance | 0.107 | 1.053 | 905 |
| *Onopordon olgae* Bunge and Schmalh. | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.28 | | 794 |
| *Oryza sativa* L. (Rice) | | | | | |
| 1 | Whole grain[g] | McCance | 0.25 | 0.31 | 1040 |
| 1 | –, germ | McCance | 0.98 | 1.30 | 1040 |
| 1 | –, endosperm | McCance | 0.004 | 0.11 | 1040 |
| 1 | –, pericarp | McCance | 0.95 | 1.04 | 1040 |
| 9 | Grain | McCance | 0.029-0.233 | 0.095-0.435 | 832 |
| 2 | Grain | CZE | 0.249-0.380 | | 746 |
| 1 | Polished grain, long[b] | McCance | 0.097 | 0.189 | 1041 |
| 2 | –, medium[b] | McCance | 0.039-0.054 | 0.080-0.128 | 1042 |
| 1 | –, short[b] | McCance | 0.038 | 0.114 | 1042 |
| 8 | White grain | McCance | 0.035-0.055 | 0.096-0.121 | 1043 |
| 8 | –, true bran | McCance | 2.231-2.637 | 2.476-2.868 | 1043 |
| 3 | Brown grain | McCance | 0.155-0.201 | 0.320-0.348 | 1044 |
| 3 | –, lightly milled | McCance | 0.100-0.118 | 0.153-0.162 | 1044 |
| 3 | –, well milled | McCance | 0.037-0.053 | 0.080-0.128 | 1044 |
| 3 | –, whole kernel | McCance | 0.239-0.253 | 0.239-0.272 | 1044 |
| 3 | –, bran | McCance | 0.660-0.810 | 1.955-2.264 | 1044 |
| 3 | Brown grain[b] | Michel | 0.10-0.28 | 0.16-0.38 | 1045 |
| 3 | –, milled | Michel | 0.02-0.07 | 0.06-0.16 | 1045 |
| 2 | –, endosperm, subaleurone | Michel | 0.21-0.24 | 0.21-0.35 | 1045 |
| 2 | –, endosperm, middle | Michel | 0.010-0.025 | 0.06-0.09 | 1045 |
| 2 | –, endosperm, inner | Michel | 0.003-0.005 | 0.05 | 1045 |
| 2 | –, bran | Michel | 0.84-2.28 | 1.00-2.60 | 1045 |
| 2 | –, polish | Michel | 0.60-1.58 | 0.67-1.61 | 1045 |
| 1 | Brown seed, unpolished | Inositol | 0.222 | | 785 |
| 1 | Brown seed, parboiled[b] | HPLC | 0.438 | | 741 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| 2 | Enriched polished seed | Harland | 0.067-0.084 | | 738 |
| 1 | Enriched seed, defatted[b] | HPLC | 0.064 | | 850 |
| 1 | Polished seed[b] | $^{31}$P NMR | 0.12 | | 743 |
| 1 | Wild seed[b] | Harland | 0.62 | | 994 |
| 12 | Seed kernel | Harland | 0.214-0.284 | 0.269-0.375 | 1046 |
| 1 | Seed, aleurone particle[c] | Inositol | 9.71 | 11.61 | 1047 |
| 1 | Seed, aleurone particle[c] | PE | 11.3 | 11.6 | 1047 |
| 1 | Seed, aleurone particle[c] | PC | + | | 1047 |
| 1 | Seed, aleurone grain | TEM/EDX | + | | 1048 |
| 1 | High-phytic seed particles | Ogawa | 18.77-18.93 | 18.77-18.93 | 800 |
| 1 | Scutellum particles | Ogawa | 19.79 | | 801 |
| 1 | Scutellar cell | TEM/EDX | + | | 1049 |
| 1 | Scutellum | SEM/EMX | + | | 1050 |
| 1 | Seed bran | GFC | + | | 778 |
| 1 | Seed bran | Harland | 0.431 | | 851 |
| 1 | Bran, stabilized[b] | HPLC | 2.20 | | 772 |
| 1 | Nonwaxy seed kernel | Harland | 0.266 | 0.340 | 1046 |
| 1 | –, embryo | Harland | 1.918 | 2.167 | 1046 |
| 1 | –, endosperm | Harland | 0.038 | 0.100 | 1046 |
| 1 | –, bran | Harland | 1.984 | 2.114 | 1046 |
| 1 | Immature grain[b,e] | Inositol | 0.0233 | | 783 |
| 1 | –, leaf, and stem | Inositol | 0.0039 | | 783 |
| 1 | –, root | Inositol | 0.00057 | | 783 |
| 1 | Sprout | McCance | 0.230 | 0.318 | 1051 |
| 2 | Leaf (straw) | Michel | 0.02 | 0.49-0.74 | 1052 |
| *Oxytropis lambertii* Pursh. (Locoweed) | | | | | |
| 1 | Seed embryo | TEM/EDX | + | | 856 |
| *Pachyrhizus erosus* (L.) Urb. (Yambean) | | | | | |
| 1 | Pod | McCance | 0.026 | 0.045 | 832 |
| 1 | Tuber | McCance | 0.015 | 0.029 | 832 |
| *Padus racemosa* Lam. (Bird Cherry) | | | | | |
| 1 | Stem cortex, 1 year old | McCance | 0.041 | | 1030 |
| *Panicum miliaceum* L. (Proso Millet) | | | | | |
| 24 | Whole seed[e] | McCance | 0.05-0.13 | | 1053 |
| 5 | –, dehulled | McCance | 0.05-0.09 | | 1053 |
| 5 | –, hull | McCance | 0.14-0.45 | | 1053 |
| 6 | Dehulled seed | McCance | 0.14-0.19 | 0.31-0.34 | 1054 |
| 1 | Seed[b] | $^{31}$P NMR | 0.21 | | 743 |
| *Panicum sumatrense* Roem. and Schult. (Little Millet) | | | | | |
| 1 | Dehusked grain | McCance | 0.058 | 0.174 | 827 |
| *Papaver somniferum* L. (Poppy) | | | | | |
| 1 | Mature seed | PC | + | | 810 |
| 1 | Defatted seed powder | Michel | 0.316 | | 758 |
| 1 | Press-cake flour[c] | McCance | 0.808 | 1.58 | 987 |
| 1 | Defatted flour [c] | McCance | 0.96 | | 1055 |
| 1 | –, protein isolate | McCance | 0.00 | | 1055 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Parkia clappertoniana* Keay (West African Locust Bean) | | | | | |
| 1 | Seed | McCance | 0.16 | 0.43 | 825 |
| *Parkinsonia aculeata* L. (Mexican Palo Verde) | | | | | |
| 1 | Seed | Harland | 0.20-0.22 | | 1028 |
| *Paspalum scrobiculatum* L. (Kodo Millet) | | | | | |
| 1 | Dehusked grain | McCance | 0.135 | 0.136 | 827 |
| *Pastinaca sativa* L. (Parsnip) | | | | | |
| 1 | Tuber | McCance | 0.016 | 0.245 | 821 |
| 1 | Tuber[b] | HPLC | 0.23 | | 741 |
| 1 | Tuber | $^{31}$P NMR | + | | 43 |
| *Peganum harmala* L. (African Rue) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.87 | | 794 |
| *Pennisetum glaucum* (L.) R.Br. (Pearl Millet) | | | | | |
| 14 | Whole grain | McCance | 0.035-0.221 | 0.245-0.348 | 1056 |
| 8 | Whole grain | McCance | 0.167-0.293 | 0.300-0.390 | 1057 |
| 2 | Whole seed | McCance | 0.179-0.306 | | 1058 |
| 1 | –, decorticated | McCance | 0.312 | | 1058 |
| 1 | –, germ | McCance | 0.752 | | 1058 |
| 1 | –, endosperm | McCance | 0.086 | | 1058 |
| 1 | –, bran | McCance | 0.278 | | 1058 |
| 1 | Whole seed meal | McCance | 0.245 | | 1058 |
| 1 | Grain flour | McCance | 0.177 | 0.311 | 1059 |
| 1 | 84-h sprout | McCance | 0.013 | | 1060 |
| *Pennisetum* spp. (Millet) | | | | | |
| 1 | Seed, flour[b] | HPLC | 0.165 | | 1061 |
| 1 | –, 48-h sprout[b] | HPLC | 0.099 | | 1061 |
| *Pentaclethra macrophylla* Benth. (African Oil Bean) | | | | | |
| 1 | Dehulled seed | McCance | 0.320 | 0.300 | 1062 |
| 1 | Hull | McCance | – | 0.040 | 1062 |
| *Perilla frutescens* (L.) Britt. (Perilla Mint) | | | | | |
| 1 | Whole flour | McCance | 0.68 | | 1063 |
| 1 | –, defatted | McCance | 1.15 | | 1063 |
| *Persea americana* Mill. (Avocado) | | | | | |
| 2 | Peeled ripe fruit | McCance | 0.35-0.69 | | 844 |
| 1 | Fruit | Harland | 0.014 | | 822 |
| *Petroselinum crispum* (Mill.) Nym. (Parsley) | | | | | |
| 1 | Leaf | McCance | 0.053 | 0.477 | 821 |
| 1 | Root[b] | Schmalfuss | 0 | 1.04 | 792 |
| *Petunia hybrida* hort. (Petunia) | | | | | |
| 1 | Pollen | $^{31}$P NMR | n.d. | | 788 |
| 3 | Flower, pollen | PE | 0.28-0.56 | | 1064 |
| 3 | –, stigma | PE | 0.08-0.17 | | 1064 |
| 3 | –, style | PE | 0-0.014 | | 1064 |
| 3 | –, ovary, filament, or petal | PE | 0 | | 1064 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Phaseolus acutifolius* Gray (Tepary Bean) | | | | | |
| 2 | Domestic bean | Harland | 0.17-0.21 | | 1028 |
| 1 | Wild bean | Harland | 0.29 | | 1028 |
| *Phaseolus coccineus* L. (Runner Bean) | | | | | |
| 1 | Bean | Harland | 0.321 | | 1065 |
| *Phaseolus lunatus* L. (Lima Bean) | | | | | |
| 18 | Bean | McCance | 0.150-0.211 | 0.316-0.480 | 1066 |
| 1 | Bean | Harland | 0.197 | | 822 |
| 2 | Seed | HPLC | 0.041-0.052 | | 900 |
| 1 | Defatted seed powder | Michel | 0.1962 | | 758 |
| 1 | Seed flour | Harland | 0.146 | | 926 |
| 1 | –, protein fraction | Harland | 0.384 | | 926 |
| 1 | –, starch fraction | Harland | 0.052 | | 926 |
| 2 | Seed protein isolate | McCance | 0.80-1.00 | | 815 |
| 1 | Seed protein isolate | DGE | + | | 815 |
| 1 | Bean crystalline protein | McCance | 0.47-1.25 | 0.46-1.20 | 1067 |
| 3 | 3-day sprout | McCance | 0.10-0.13 | 0.28-0.35 | 980 |
| *Phaseolus vulgaris* L. (Bean (Common)) | | | | | |
| 10 | Whole bean | McCance | 0.33-0.82 | | 1068 |
| 10 | –, dehulled | McCance | 0.46-1.03 | | 1068 |
| 50 | Whole bean | McCance | 0.15-0.44 | 0.259-0.556 | 1069 |
| ~15 | Bean | McCance | 0.139-0.373 | 0.295-0.514 | 969 |
| 1 | Bean flour | McCance | 0.75 | | 1070 |
| 1 | –, CDF fraction | McCance | 1.55 | | 1070 |
| 1 | Immature bean | McCance | 0.0014-0.0120 | 0.0843-0.2688 | 1071 |
| 2 | Bean[b] | HPLC | 0.25-0.48 | | 772 |
| 1 | Bean, defatted[b] | HPLC | 0.39 | | 850 |
| 1 | Bean | Inositol | 0.484 | | 784 |
| 1 | Bean, axis | $^{31}$P NMR | 0.335 | 0.675 | 824 |
| 1 | –, cotyledon | $^{31}$P NMR | 0.383 | 0.453 | 824 |
| 3 | Dehulled bean | Harland | 0.392-0.467 | 0.493-0.535 | 1072 |
| 3 | –, protein fraction | Harland | 0.668-0.851 | 0.844-0.916 | 1072 |
| 3 | –, starch fraction | Harland | 0.121-0.246 | 0.274-0.400 | 1072 |
| 3 | –, hull | Harland | 0.288-0.382 | 0.447-0.507 | 1072 |
| 5 | Bean protein concentrate | McCance | 0.132-0.428 | | 1073 |
| 2 | Bean protein isolate | McCance | 1.11-1.36 | | 815 |
| 2 | Bean protein isolate | DGE | + | | 815 |
| 2 | Bean crystalline protein | McCance | 0.79-2.16 | 0.74-2.16 | 1067 |
| 1 | Pod | McCance | 0.005-0.012 | | 754 |
| 1 | Seedling, embryonic axis[f] | McCance | 0.0030 | | 888 |
| 1 | –, vacuole[f] | McCance | 0 | | 888 |
| *Philydrella pygmaea* (R.Br.) Caruel | | | | | |
| 1 | Corm, seed | Microscopy | + | | 1000 |
| 1 | Corm | SEM/EMX | + | | 1000 |
| 1 | Corm | TEM | + | | 1000 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Phoenix dactylifera* L. (Date Palm) | | | | | |
| 1 | Seed | McCance | 0.023 | | 865 |
| 1 | Defatted seed powder | Michel | 0.0232 | | 758 |
| 1 | Haustoria | Microscopy | + | | 1074 |
| 1 | Haustoria | TEM/EDX | + | | 1074 |
| 1 | Deseeded fruit | McCance | 0.04 | 0.18 | 855 |
| *Phylloglossum drummondii* Kunze | | | | | |
| 1 | Stem tuber | Microscopy | + | | 1000 |
| 1 | Stem tuber | SEM, TEM | + | | 1000 |
| *Physalis ixocarpa* Brot. (Tomatillo) | | | | | |
| 1 | Whole fruit | McCance | 0.084 | 0.482 | 827 |
| *Physalis peruviana* L. (Cape Gooseberry) | | | | | |
| 1 | Whole fruit | McCance | 0.107 | 0.440 | 827 |
| *Picea glauca* (Moench) Voss (White Spruce) | | | | | |
| 1 | Whole seed | Harland | 0.688 | 0.782 | 1075 |
| 1 | –, kernel | Harland | 0.936 | 1.151 | 1075 |
| 1 | –, zygotic embryo | Harland | 0.347 | 1.070 | 1075 |
| 1 | –, female gametophyte | Harland | 1.014 | 1.163 | 1075 |
| 1 | Seed, cotyledon | TEM/EDX | | + | 1076 |
| 1 | –, hypocotyl | TEM/EDX | | + | 1076 |
| 1 | –, radicle | TEM/EDX | | + | 1076 |
| *Picea mariana* (Mill.) Brit., St. and Pog. (Black Spruce) | | | | | |
| 1 | Needle and stem | McCance | negl.[j] | | 833 |
| *Picea pungens* Engelm. (Colorado Spruce) | | | | | |
| 1 | Pollen | FTIR | + | 0.16 | 818 |
| 1 | Pollen | McCance | 0.1075 | 0.16 | 818 |
| *Picea* spp. (Spruce) | | | | | |
| 1 | Seed[b,c] | Posternak | 0.600 | 0.656 | 807 |
| 1 | –, aleurone grain[b,c] | Posternak | 2.58 | 2.67 | 807 |
| *Pinus banksiana* Lamb. (Jack Pine) | | | | | |
| 1 | Seed cotyledon | TEM/EDX | + | | 1077 |
| 1 | Seedling cotyledon | TEM/EDX | + | | 1077 |
| *Pinus canariensis* C. Sm. (Canary Island Pine) | | | | | |
| 1 | Pollen | PE | 0.07 | 0.50 | 1078 |
| *Pinus cembra* L. (Swiss Stone Pine) | | | | | |
| 1 | Pollen | PE | 0.05 | 0.46 | 1078 |
| *Pinus contorta* Douglas ex Louden (Lodgepole Pine) | | | | | |
| 1 | Seed cotyledon, hypocotyl, and root | TEM/EDX | + | | 1079 |
| *Pinus coulteri* D. Don (Coulter Pine) | | | | | |
| 1 | Seed cotyledon, hypocotyl, and root | TEM/EDX | + | | 1079 |
| *Pinus flexilis* James (Limber Pine) | | | | | |
| 1 | Pollen | PE | 0.03 | 0.40 | 788 |
| *Pinus griffithii* McClelland (Himalayan Pine) | | | | | |
| 1 | Pollen | PE | 0.03 | 0.46 | 1078 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Pinus koraiensis* Sieb. and Zucc. (Korean Pine) | | | | | |
| 1 | Seed cotyledon, hypocotyl, and root | TEM/EDX | + | | 1079 |
| *Pinus mugo* Turra (Mugo Pine) | | | | | |
| 1 | Seed cotyledon, hypocotyl, and root | TEM/EDX | + | | 1079 |
| 1 | Pollen | PE | <0.01 | 0.54 | 1078 |
| *Pinus mugo* ssp. *mughus* Scop. | | | | | |
| 1 | Pollen | PE | <0.01 | 0.50 | 1078 |
| *Pinus mugo* ssp. *rostrata* (Ant.) Hoopes | | | | | |
| 1 | Pollen | PE | 0.11 | 0.43 | 1078 |
| *Pinus nigra* Black Pine | | | | | |
| 1 | Seed cotyledon, hypocotyl, and root | TEM/EDX | + | | 1079 |
| *Pinus pinea* L. (Italian Stone Pine) | | | | | |
| 1 | Pollen | PE | <0.01 | 0.31 | 1078 |
| *Pinus ponderosa* (Dougl. ex) Laws. (Ponderosa Pine) | | | | | |
| 1 | Seed cotyledon, hypocotyl, and root | TEM/EDX | + | | 1079 |
| 1 | Pollen | McCance | 0.0076 | 0.017 | 818 |
| 1 | Pollen | FTIR | + | 0.017 | 818 |
| 1 | Fallen needle | Inositol | + | | 1080 |
| *Pinus radiata* D. Don (Monterey Pine) | | | | | |
| 1 | Pollen | PE | 0.02 | 0.37 | 1078 |
| 1 | Needle (leaf) | PE | <0.0008 | 0.22 | 1078 |
| 1 | Seed | PE | 0.79 | 0.78 | 1078 |
| *Pinus resinosa* Ait. (Red Pine) | | | | | |
| 1 | Seed cotyledon, hypocotyl, and root | TEM/EDX | + | | 1079 |
| *Pinus sabiniana* Douglas | | | | | |
| 1 | Seed cotyledon, hypocotyl, and root | TEM/EDX | + | | 1079 |
| *Pinus strobus* L. (Eastern White Pine) | | | | | |
| 1 | Seed cotyledon, hypocotyl, and root | TEM/EDX | + | | 1079 |
| *Pinus sylvestris* L. (Scotch Pine) | | | | | |
| 1 | Seed cotyledon, hypocotyl, and root | TEM/EDX | + | | 1079 |
| *Pinus yunnanensis* Franchet (Yunnan Pine) | | | | | |
| 1 | Pollen | PE | 0.04 | 0.40 | 1078 |
| *Pinus* spp. (Pine) | | | | | |
| 1 | Nut | McCance | 0.318 | 0.514 | 1081 |
| *Piper clusii* C. DC (African Cubeb) | | | | | |
| 1 | Seed | McCance | 0.064 | 0.422 | 821 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Piper guineense* Schum. and Thonn. (Etinkene (Guinea Cubeb)) | | | | | |
| 1 | Leaf | McCance | 0.055 | 0.215 | |
| *Piper nigrum* L. (Black Pepper) | | | | | |
| 1 | Seed | McCance | 0.132 | 0.226 | 821 |
| *Pisonia alba* Span. (Lettuce Tree) | | | | | |
| 1 | Leaf | McCance | 0.007 | 0.010 | 832 |
| *Pistacia atlantica* Desf. (Mt. Atlas Mastic Tree) | | | | | |
| 1 | Defatted seed powder | Michel | 0.176 | | 758 |
| *Pistacia chinensis* Bunge (Chinese Pistachio) | | | | | |
| 1 | Pollen | PE | 0.07 | 0.56 | 788 |
| *Pistacia vera* L. (Pistachio) | | | | | |
| 1 | Shelled nut[b,e] | McCance | 0.164 | 0.529 | 937 |
| 1 | Seed cotyledon | TEM/EDX | + | | 843 |
| *Pisum sativum* L. (Peas) | | | | | |
| ~15 | Seed | McCance | 0.092-0.311 | 0.234-0.528 | 969 |
| 15 | Seed | Harland | 0.178-0.376 | | 1082 |
| 1 | Seed | CZE | 0.619 | | 700 |
| 2 | Seed | PC | + | | 1083 |
| 1 | Whole pea | McCance | 0.221 | | 1084 |
| 1 | –, cotyledon | McCance | 0.220 | | 1084 |
| 1 | –, germ | McCance | 0.345 | | 1084 |
| 1 | –, hull | McCance | 0.003 | | 1084 |
| 2 | Pea, interior region[b,c] | McCance | 0.20-0.50 | | 1085 |
| 2 | –, exterior region[b,c] | McCannce | 0.30-0.64 | | 1085 |
| 1 | Pea flour | McCance | 0.601 | 0.883 | 1086 |
| 3 | –, protein flour | McCance | 0.56-0.63 | 1.05-1.20 | 1087 |
| 1 | Pea, protein fraction | McCance | 0.53 | 0.86 | 1088 |
| 1 | –, starch fraction | McCance | 0.06 | 0.09 | 1088 |
| 1 | Seed flour | Harland | 0.209 | | 926 |
| 1 | –, protein fraction | Harland | 0.532 | | 926 |
| 1 | –, starch fraction | Harland | 0.051 | | 926 |
| 1 | Immature pea | McCance | 0.045-0.048 | | 1089 |
| 2 | Individual peas[c] | McCance | 0.35-0.43 | | 1090 |
| 3 | Whole seed | Harland | 0.21-0.26 | | 1091 |
| 2 | –, protein concentrate | Harland | 0.37-0.53 | | 1091 |
| 1 | Acid-washed fiber | Harland | 0.014 | | 851 |
| 1 | Pea, split[b] | HPLC | 0.473 | | 741 |
| 1 | Seed, axis[a] | $^{31}$P NMR | 60 | | 824 |
| 1 | –, cotyledon[a] | $^{31}$P NMR | 82 | | 824 |
| 1 | Seed cotyledon | SEM/EDX | + | | 706 |
| 1 | Seed cotyledon | TEM/EDX | + | | 706 |
| 1 | Root | SEM/EMX | + | | 891 |
| *Pithecellobium dulce* (Roxb.) Benth. (Korukapalli (Manila Tamarind)) | | | | | |
| 1 | Leaf | McCance | 0 | 0.394 | 821 |
| 1 | Peeled deseeded fruit | McCance | 0 | 0.309 | 827 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Pithecellobium flexicaule* (Benth.) Coult. (Ébano) | | | | | |
| 1 | Seed cotyledon, immature | McCance | 0.22 | | 1092 |
| 1 | –, mature | McCance | 0.76 | | 1092 |
| *Poa annua* L. (Annual Bluegrass) | | | | | |
| 1 | Root | GFC | 0.05 | 0.210 | 696 |
| 1 | Root | HPLC | n.d. | 0.210 | 696 |
| *Portulaca oleracea* L. (Purslane) | | | | | |
| 1 | Stem and leaf | McCance | 0.036 | 0.482 | 827 |
| 1 | Leaf | McCance | 0.009 | 0.053 | 832 |
| *Potentilla asiatica* Juz. (Cinquefoil) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.65 | | 794 |
| *Poterium polygamum* Waldst. and Kit. | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.56 | | 795 |
| *Premna odorata* Blanco (Premna) | | | | | |
| 1 | Leaf | McCance | 0.035 | 0.068 | 832 |
| *Prosopis africana* (Gui., Per., and Rich.) Taub. | | | | | |
| 1 | Seed | McCance | 0.25 | 0.47 | 825 |
| *Prosopis chilensis* (Mol.) Stuntz. (Algarrobo) | | | | | |
| 1 | Seed | McCance | 0.13 | 0.48 | 825 |
| *Prosopis glandulosa* Torr. (Honey Mesquite) | | | | | |
| 1 | –, seed | Harland | 0.282 | 0.31 | 1093 |
| 1 | –, pericarp | Harland | 0.006 | 0.08 | 1093 |
| 1 | Seed[c] | Inositol | 0.24 | | 1094 |
| 1 | –, pericarp | Inositol | 0 | | 1094 |
| 1 | Green pod | Harland | 0.044 | 0.11 | 1093 |
| 1 | Mature pod | Harland | 0.046 | 0.13 | 1093 |
| *Prosopis velutina* Woot. (Velvet Mesquite) | | | | | |
| 1 | Seed[c] | Inositol | 0.25 | | 1094 |
| 1 | –, pericarp | Inositol | 0 | | 1094 |
| 1 | Fallen leaf | Inositol | + | | 1080 |
| *Protea compacta* R.Br. | | | | | |
| 1 | Cotyledon | SEM/EDX | + | | 1095 |
| *Prunus armeniaca* L. (Apricot) | | | | | |
| 1 | Defatted kernel flour | McCance | 0.0039 | 0.667 | 1096 |
| 1 | Kernel protein isolate[b,c] | McCance | 0.51 | 0.65 | 1097 |
| *Prunus avium* (L.) L. (Cherry) | | | | | |
| 1 | Fruit[b] | McCance | 0.013 | | 931 |
| *Prunus bucharica* Korsh. | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 1.04 | | 795 |
| *Prunus domestica* L. (Plum) | | | | | |
| 1 | Flesh and skin | McCance | 0 | 0.265 | 827 |
| 1 | Kernel protein isolate[b,c] | McCance | 0.14 | 0.32 | 1097 |
| *Prunus dulcis* (Mill.) D.A. Webb (Almond) | | | | | |
| 1 | Nut | McCance | 0.242 | 0.645 | 842 |
| 1 | Seed | Harland | 0.60 | | 761 |
| 1 | Seed cotyledon | TEM/EDX | + | | 879 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Prunus laurocerasus* L. (Cherry Laurel) | | | | | |
| 1 | Fat-free leaf flour[b,c] | Michel | 0.023-0.045 | | 757 |
| *Prunus mahaleb* L. (Mahaleb Cherry) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.62 | | 795 |
| *Prunus persica* (L.) Batsch. (Peach) | | | | | |
| 1 | Flesh and skin | McCance | 0.008 | 0.325 | 827 |
| 1 | Defatted kernel flour[c] | McCance | 0.0149 | | 1098 |
| 1 | Kernel protein isolate[b,c] | McCance | 0.30 | 0.33 | 1097 |
| *Prunus petunnikowii* Litv. | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.98 | | 795 |
| *Psidium guajava* L. (Guava) | | | | | |
| 1 | Peeled ripe fruit | McCance | 0.76 | | 844 |
| *Psophocarpus tetragonolobus* (L.) DC (Winged Bean) | | | | | |
| 16 | Whole seed[e] | McCance | 0.172-0.212 | | 1099 |
| 12 | Seed | Harland | 0.219-0.339 | 0.433-0.632 | 1100 |
| 3 | Whole seed | McCance | 0.179-0.202 | 0.263-0.278 | 1101 |
| 12 | Defatted seed flour[e] | McCance | 0.28-0.48 | 0.36-0.64 | 1102 |
| 1 | –, protein concentrate[e] | McCance | 0.13 | | 1102 |
| 1 | Hull[e] | McCance | <0.03 | | 1102 |
| *Psoralea drupacea* Bunge | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.36 | | 795 |
| *Pterocarpus mildbraedii* Harms. (Mkpa) | | | | | |
| 1 | Leaf | McCance | 0.072 | 0.410 | 981 |
| *Pterocarpus osun* Craib. (African Padauk) | | | | | |
| 1 | Seed | McCance | 0.28 | 0.46 | 825 |
| *Punica granatum* L. (Pomegranate) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.53 | | 796 |
| *Quercus lusitanica* Lam. (Portuguese Oak) | | | | | |
| 1 | Pollen | PE | 0.15 | 0.56 | 788 |
| *Quercus robur* L. (English Oak) | | | | | |
| 1 | Pollen | PE | 0.18 | 0.56 | 788 |
| *Quercus* spp. (Oak) | | | | | |
| 1 | Fat-free acorn flour[b,c] | Michel | 0.01 | | 757 |
| *Ranunculus* spp. (Buttercup) | | | | | |
| 1 | Seed[b] | McCance | 0.32 | 0.46 | 1015 |
| *Raphanus sativus* L. (Radish) | | | | | |
| 1 | Defatted seed powder | Michel | 0.071 | | 758 |
| 2 | Tuber | McCance | 0 | 0.208-0.447 | 821 |
| 1 | Defatted tuber flour | McCance | 0.2047 | 1.870 | 1103 |
| 1 | Root | SEM/EMX | + | | 891 |
| *Rauvolfia vomitoria* Afzel. (Swizzlestick) | | | | | |
| 1 | Seed | McCance | 0.099 | | 828 |
| *Rhaponticum integrifolium* C. Winkl. | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.28 | | 794 |
| *Rhodomyrtus tomentosa* (Ait.) Hassk. (Downy Myrtle) | | | | | |
| 1 | Cored fruit | McCance | 0.058 | 0.079 | 827 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Rhus hirta* (L.) Sudw. (Staghorn Sumac) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.79 | | 796 |
| *Ricinus communis* L. (Castor Bean) | | | | | |
| 1 | Immature seed | McCance | 10.2 | | 1104 |
| 1 | Bean | TLC | + | | 813 |
| 1 | Defatted flour[b,c] | McCance | 1.7 | | 943 |
| 1 | Seed, aleurone grain | McCance | 2.90 | | 1023 |
| 1 | –, globoid | McCance | 17.2 | | 1023 |
| 1 | Defatted seed powder | Michel | 0.5086 | | 758 |
| 2 | Seed endosperm | Microscopy | + | | 819,1105,1106 |
| 1 | Seed endosperm | SEM/EDX | + | | 1105 |
| *Roemeria refracta* DC (Roemer Poppy) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 1.21 | | 794 |
| *Rosa canina* L. (Dog Rose) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.70 | | 794 |
| *Rosa rubiginosa* L. (Sweetbrier Rose) | | | | | |
| 1 | Defatted seed flour | McCance | 0.046 | 0.167 | 1107 |
| 1 | Deseeded fruit | McCance | Trace | 0.034 | 1108 |
| *Rubia tinctorum* L. (Madder) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.17 | | 796 |
| *Rubus* spp. (Blackberry) | | | | | |
| 1 | Fruit[d,f] | McCance | 0.0042 | 0.0259 | 735 |
| *Rumex acetosa* L. (Sorrel) | | | | | |
| 1 | Leaf | McCance | 0.063 | | 1109 |
| *Rumex halaczii* Rech. | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.17 | | 796 |
| *Rumex vesicarius* L. (Chukai Shak) | | | | | |
| 1 | Leaf | McCance | 0.0015 | | 902 |
| *Saccharum officinarum* L. (Sugarcane) | | | | | |
| 1 | Acid-washed fiber | Harland | 0 | | 851 |
| *Salvia macrosiphon* Boiss. (Sage) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 1.07 | | 796 |
| *Sandoricum koetjape* (Burm. f.) Merr. (Santol) | | | | | |
| 1 | Fruit | | 0.008 | 0.026 | 832 |
| *Santalum acuminatum* R.Br. (Quandong) | | | | | |
| 1 | Endosperm | TEM/EDX | + | | 879 |
| *Saposhnikovium* spp. | | | | | |
| 1 | Root | PE | + | | 779 |
| *Secale cereale* L. (Rye) | | | | | |
| 3 | Grain[b,g] | McCance | 0.29-0.53 | | 907 |
| 2 | Grain | CZE | 0.151-0.160 | | 746 |
| 1 | Seed | Michel | 0.197 | 0.342 | 996 |
| 1 | Seed | HPLC | 0.28 | | 774 |
| 1 | Whole grain[b,c] | Harland | 0.41 | | 933 |
| 4 | Whole grain[g] | McCance | 0.188-0.284 | | 1110 |
| 1 | –, kernel, upper half | McCance | 0.226 | | 1110 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| 1 | –, kernel, germ half | McCance | 0.296 | | 1110 |
| 2 | –, coarse bran | McCance | 1.020-1.217 | | 1110 |
| 2 | –, fine bran | McCance | 0.227-0.809 | | 1110 |
| 4 | Seed flour[g] | McCance | 0.080-0.118 | | 1110 |
| 1 | Seed flour, 100% extraction | McCance | 0.23 | 0.37 | 1111 |
| 1 | –, 65% extraction | McCance | 0.01 | 0.15 | 1111 |
| 1 | Seed aleurone cell | SEM | + | | 870 |
| 1 | Pollen | PE | 0 | 0.62 | 788 |
| *Senecio cruentus* DC (Cineraria) | | | | | |
| 1 | Pollen | PE | 0 | 0.59 | 788 |
| *Sesamum indicum* L. (Sesame) | | | | | |
| 1 | Seed | McCance | 0.239 | 0.461 | 832 |
| 1 | Seed meal[b] | McCance | 1.00 | 1.4 | 1112 |
| 1 | Defatted seed meal[b] | McCance | 1.44 | | 699 |
| 1 | Defatted seed meal[b] | DGE | + | | 699 |
| 1 | Seed, dehulled, and defatted[b] | HPLC | 1.51 | | 850 |
| 1 | Seed protein concentrate | McCance | 0.181 | | 1113 |
| 5 | Seed protein isolate | McCance | 0.21 | 0.38 | 1114 |
| 1 | Seed β-globulin[c] | Harland | n.d. | 0.06 | 1115 |
| *Sesbania grandiflora* (L.) Poir. (Agati (Scarlet Wistaria Tree)) | | | | | |
| 1 | Leaf | McCance | 0 | 0.355 | 821 |
| 1 | Flower | McCance | 0.021 | 0.024 | 832 |
| *Sesuvium portulacastrum* L. (Sea Purslane) | | | | | |
| 1 | Leaf | McCance | 0.013 | 0.038 | 832 |
| *Setaria italica* (L.) Beauv. (Italian (Foxtail) Millet) | | | | | |
| 1 | Seed | McCance | 0.237 | 0.356 | 821 |
| 4 | Dehulled seed | McCance | 0.18-0.20 | 0.17-0.36 | 1054 |
| *Simmondsia chinensis* (Link.) Schneid. (Jojoba) | | | | | |
| 1 | Seed cotyledon | TEM/EDX | + | | 962 |
| 1 | Defatted meal[c] | McCance | 0.002 | | 1116 |
| 1 | Decorticated meal[c] | McCance | 0.003 | | 1116 |
| 1 | Seed protein concentrate[c] | McCance | n.d. | | 1116 |
| 1 | Germinated seed | $^{31}$P NMR | + | | 43 |
| *Sinapis alba* L. (White Mustard) | | | | | |
| 1 | Defatted seed flour | McCance | 0.90 | | 881 |
| 1 | Defatted seed powder | Michel | 0.3924 | | 758 |
| 1 | Seed, aleurone grain | McCance | 1.49 | | 1023 |
| *Solanum africanum* Mill. | | | | | |
| 1 | Leaf | McCance | 0.050 | 0.8 | 909 |
| *Solanum gnomalum* | | | | | |
| 1 | Leaf and stem | McCance | 0.033 | 0.192 | 837 |
| *Solanum mauritianum* Scop. (Earleaf Nightshade) | | | | | |
| 1 | Pollen | PE | 0.31 | 0.40 | 788 |
| *Solanum melongena* L. (Eggplant) | | | | | |
| 1 | Vegetable | McCance | 0.055 | 0.504 | 821 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Solanum nigrum* L. (Black Nightshade) | | | | | |
| 1 | Leaf | McCance | 0.045 | 0.9 | 909 |
| *Solanum tuberosum* L. (Potato) | | | | | |
| 1 | Leaf[b] | Suzuki | 0.096 | 0.433 | 798 |
| 5 | Tuber | McCance | 0.055-0.068 | 0.205-0.266 | 667 |
| 1 | Tuber[b] | HPLC | 0.10 | 0.230 | 696 |
| 1 | Tuber | GFC | 0.04 | 0.230 | 696 |
| 1 | Tuber[b] | $^{31}$P NMR | 0.03 | | 743 |
| 1 | Tuber, stem end[e] | McCance | 0.0043 | 0.0281 | 1117 |
| 1 | –, rose end[e] | McCance | 0.0091 | 0.0400 | 1117 |
| 2 | Tuber | PC | + | 0.062-0.079 | 315 |
| 2 | Tuber, mature[b,c] | Harland | 0.0149-0.0160 | 0.0616-0.0717 | 1118 |
| 2 | –, immature[b,c] | Harland | 0.0090-0.0103 | 0.053-0.062 | 1118 |
| 1 | Tuber, pith | $^{31}$P NMR | + | | 43 |
| 1 | –, other parts | $^{31}$P NMR | n.d. | | 43 |
| *Sophora japonica* L. (Japanese Pagoda Tree) | | | | | |
| 1 | Seed meal, defatted | Mukhamedova | 0.42 | | 795 |
| 1 | Seed, axis[a] | $^{31}$P NMR | 79 | | 824 |
| 1 | –, hypocotyl[a] | $^{31}$P NMR | 90 | | 824 |
| *Sorghum bicolor* (L.) Moench (Sorghum) | | | | | |
| 16 | Whole grain | McCance | 0.12-0.18 | 0.28-0.50 | 1119 |
| 30 | Whole grain | McCance | 0.172-0.407 | 0.224-0.480 | 756 |
| 6 | –, dehulled grain | McCance | 0.05-0.18 | 0.09-0.22 | 756 |
| 6 | –, bran | McCance | 0.73-1.16 | 0.84-1.31 | 756 |
| 7 | Whole grain[b] | McCance | 0.20-0.37 | | 1120 |
| 7 | –, germ | McCance | 0.54-1.91 | | 1120 |
| 7 | –, bran | McCance | 0.19-0.49 | | 1120 |
| 7 | –, grits (endosperm) | McCance | 0.02-0.18 | | 1120 |
| 2 | Grain | McCance | 0.160-0.273 | 0.223-0.307 | 1121 |
| 1 | Grain | Harland | 0.249 | | 936 |
| 1 | Whole grain[b] | Inositol | + | | 1120 |
| 4 | Pearled grain | HPLC | 0.06-0.28 | | 765 |
| 2 | Grain pearling | HPLC | 0.31-0.34 | | 765 |
| 1 | Seed aleurone tissue | Microscopy | + | | 868 |
| 1 | 5 ft plant, entire panicle[b] | Harland | 0.040 | 0.30 | 867 |
| 1 | –, 11th leaf blade | Harland | 0.009 | 0.22 | 867 |
| 1 | –, root | Harland | 0.009 | 0.17 | 867 |
| *Sorghum halepense* (L.) Pers. (Johnson Grass) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.45 | | 796 |
| *Sphenostylis stenocarpa* (Hochst ex A. Rich) Harms (African Yambean) | | | | | |
| 1 | Seed | McCance | 0.174 | 0.248 | 1122 |
| 3 | Bean | Harland | 0.178-0.215 | 0.267-0.303 | 1123 |
| 1 | Seed | HPLC | 0.016 | | 900 |
| *Spinacia oleracea* L. (Spinach) | | | | | |
| 1 | Stalk | McCance | 0 | 0.229 | 821 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| 1 | Leaf | McCance | 0.010 | 0.360 | 821 |
| 1 | Mature leaf, cytosol | $^{31}$P NMR | + | | 50 |
| 1 | –, chloroplast | $^{31}$P NMR | 0 | | 50 |
| *Spinacia turkestanica* Iljin | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.25 | | 796 |
| *Spirodela polyrrhiza* (L.) Schleid. (Giant Duckweed) | | | | | |
| 1 | Pulp | McCance | 0.146 | | 876 |
| 1 | Juice | McCance | 0.098 | | 876 |
| 1 | Leaf protein concentrate | McCance | 0.163 | | 876 |
| *Spondias mombin* L. (Yellow Mombin) | | | | | |
| 1 | Seed | McCance | 0.234 | | 828 |
| *Spondias purpurea* L. (Red Mombin) | | | | | |
| 1 | Young leaf | McCance | 0.056 | 0.099 | 832 |
| 1 | Fruit | McCance | 0.008 | 0.036 | 832 |
| *Sterculia foetida* L. (Indian Almond, Jangli Badam) | | | | | |
| 1 | Kernel | McCance | 0.306 | 0.644 | 827 |
| *Stillingia* spp. (Toothleaf) | | | | | |
| 1 | Defatted seed flour[b,c] | McCance | 1.8 | | 943 |
| *Stizolobium aterrimum* Piper and Tracy (Bengal Bean) | | | | | |
| 1 | Boiled bean | Harland | 0.146 | | 822 |
| *Strelitzia reginae* (Banks.) Ait. (Bird-of-Paradise) | | | | | |
| 1 | Pollen | PE | 0.15 | 0.74 | 788 |
| *Stylidium petiolare* Sond. | | | | | |
| 1 | Corm, seed | Microscopy | + | | 1000 |
| 1 | Corm | SEM/EMX | + | | 1000 |
| 1 | Corm | TEM | + | | 1000 |
| *Talinum triangulare* (Jacq.) Willd. (Fameflower, Philippine Spinach) | | | | | |
| 1 | Leaf | McCance | 0.004 | 0.018 | 832 |
| *Tamarindus indica* L. (Tamarind) | | | | | |
| 1 | Seed | McCance | 0.013 | 0.165 | 1124 |
| 1 | –, pulp | McCance | n.d. | 0.091 | 1124 |
| 1 | Unripe seed[e] | McCance | 0 | 0.101 | 842 |
| 1 | Leaf and stem | McCance | 0 | 0.475 | 827 |
| 1 | Young leaf | McCance | 0.008 | 0.023 | 832 |
| 1 | Unripe fruit | McCance | 0.016 | 0.034 | 832 |
| 1 | Flower | McCance | 0.004 | 0.050 | 832 |
| *Telfairia occidentalis* Hook. f. (Fluted Pumpkin) | | | | | |
| 1 | Leaf | McCance | 0.15 | 1.2 | 840 |
| *Terminalia catappa* L. (Indian Almond) | | | | | |
| 1 | Seed | McCance | 0.449 | | 828 |
| *Tetracarpidium conophorum* (Müll. Arg.) Hutch. and Dalz. (Conophor) | | | | | |
| 1 | Boiled seed | | 0.063 | 0.774 | 1125 |
| *Tetrapleura tetraptera* (Schum. and Thonn.) Taub | | | | | |
| 1 | Seed | McCance | 0.16 | 0.21 | 825 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Tetrastigma harmandii* Planch. (Ayo) | | | | | |
| 1 | Leaf | McCance | 0.020 | 0.080 | 832 |
| *Theobroma cacao* L. (Cocoa) | | | | | |
| 1 | Bean[b,c] | Suzuki | 0.24 | 0.37 | 799 |
| 1 | –, shell[b,c] | Suzuki | 0.29 | 0.52 | 799 |
| 1 | –, powder[b,c] | Suzuki | 0.47 | 0.63 | 799 |
| 1 | Husk | HPLC | 0.28 | 0.69 | 1126 |
| *Treculia africana* Decne. (African Breadfruit) | | | | | |
| 1 | Seed | McCance | 0.002 | 0.382 | 1127 |
| *Trichodesma incanum* (Bunge) DC | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.34 | | 794 |
| *Trichosanthes anguina* L. (Snake Gourd) | | | | | |
| 1 | Gourd[e] | McCance | 0 | 0.029 | 842 |
| *Trifolium pratense* L. (Red Clover) | | | | | |
| 1 | Defatted meal[b] | Schmalfuss | 0 | 2.23 | 791 |
| 1 | Herbage[g] | Kazakov | 0.13 | | 803 |
| 1 | Root | McCance | 0.009 | 0.44 | 1016 |
| *Trifolium repens* L. (White (Ladino) Clover) | | | | | |
| 1 | Whole plant (full bloom)[b] | Harland | 0.009 | 0.28 | 867 |
| 1 | Radicle | Microscopy | + | | 1128 |
| *Trifolium* spp. (Clover) | | | | | |
| 1 | Seed[b,g] | McCance | 0.29 | 0.56 | 1129 |
| *Trigonella foenum-graecum* L. (Fenugreek) | | | | | |
| 2 | Seed | McCance | 0.173-0.207 | 0.321-0.418 | 1018 |
| 1 | Seed | Harland | 0.047 | 0.284 | 1130 |
| 1 | Seed, cotyledon | McCance | 0.08 | | 1131 |
| 1 | –, axis | McCance | 0.03 | | 1131 |
| 1 | –, endosperm | McCance | 0.01 | | 1131 |
| 1 | Leaf | McCance | 0.90 | 1.0 | 840 |
| 2 | Sprout | McCance | 0.087-0.112 | 0.174-0.280 | 1018 |
| *Triticum aestivum* L. (Wheat) | | | | | |
| 38 | Seed | McCance | 0.174-0.380 | 0.289-0.524 | 858 |
| 21 | Whole grain[c] | McCance | 0.152-0.328 | 0.233-0.378 | 1132 |
| 19 | Whole grain | McCance | 0.148-0.298 | 0.310-0.490 | 1133 |
| 8 | Seed flour[b,g] | McCance | 0.19-0.36 | | 907 |
| 10 | Grain, dryland crop[j] | McCance | 0.233-0.286 | 0.323-0.359 | 1134 |
| 10 | –, irrigated crop[j] | McCance | 0.270-0.342 | 0.342-0.401 | 1134 |
| 24 | Grain | HPLC | 0.092-0.280 | 0.225-0.424 | 1135 |
| 12 | Grain[c] | McCance | 0.109-0.318 | 0.190-0.449 | 1136 |
| 5 | Grain[b] | McCance | 0.12-0.32 | 0.19-0.44 | 859 |
| 1 | Grain | CZE | 0.109 | | 746 |
| 1 | Grain | PC | + | | 811 |
| 1 | Seed | Mössbauer | + | | 816 |
| 1 | Seed protein body | Morton | 1.2 | 0.96 | 805 |
| 1 | Seed protein concentrate[b,e] | McCance | 0.347-0.696 | 0.486-1.383 | 733 |
| 1 | Pollard seed[b] | McCance | 0.277-0.962 | 0.350-1.238 | 826 |
| 1 | Soft, whole kernel[g] | McCance | 0.32 | 0.42 | 1040 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| 1 | –, germ | McCance | 1.10 | 1.66 | 1040 |
| 1 | –, endosperm | McCance | 0.001 | 0.11 | 1040 |
| 1 | –, hull | McCance | 0 | 0.08 | 1040 |
| 1 | –, aleurone | McCance | 1.16 | 1.39 | 1040 |
| 3 | Aleurone tissue | Microscopy | + | | 819,868,1137 |
| 1 | Aleurone cell | SEM | + | | 870 |
| 2 | Aleurone grain | TEM | + | | 868 |
| 6 | Defatted seed powder | Michel | 0.145-0.200 | | 758 |
| 8 | Whole seed[b] | Michel | 0.252-0.371 | 0.341-0.498 | 759 |
| 8 | –, flour[b] | Michel | 0.024-0.060 | 0.092-0.134 | 759 |
| 8 | –, gliadin[b] | Michel | 0.008-0.036 | 0.081-0.184 | 759 |
| 8 | –, glutenin[b] | Michel | 0.044-0.083 | 0.208-0.314 | 759 |
| 8 | –, gluten[b] | Michel | 0.003-0.087 | 0.213-0.281 | 759 |
| 9 | Seed | Harland | fig. | 0.463-0.550 | 830 |
| 5 | Seed | GFC, PE | + | | 1138 |
| 1 | Seed flour[b] | Harland | 0.06-0.07 | | 734 |
| 2 | Seed Waldron bran[b] | Harland | 0.96-1.31 | | 738 |
| 1 | Seed germ | Harland | 0.63 | | 761 |
| 1 | Seed embryo | TEM/EDX | + | | 1139 |
| 1 | Whole grain[b] | HPLC | 0.30 | | 774 |
| 1 | Break flour | HPLC | <0.02 | | 777 |
| 1 | Germ, defatted[b] | HPLC | 0.68 | | 850 |
| 1 | Whole grain[b] | $^{31}$P NMR | 0.876 | | 873 |
| 3 | Grain, 100% extraction[c] | $^{31}$P NMR | 0.24-0.27 | | 743 |
| 1 | –, flour[b] | $^{31}$P NMR | 0.036 | | 743 |
| 1 | –, bran[b] | $^{31}$P NMR | 0.96 | | 743 |
| 1 | Seed flour[b] | Inositol | 0.077 | | 784 |
| 1 | –, germ tailings | Inositol | 0.896 | | 784 |
| 1 | Seed flour | Phytase | 0.498 | | 1140 |
| 1 | Seed gluten[b] | McCance | 0.060 | | 1141 |
| 15 | Bran | HPLC | 0.72-1.67 | | 1142 |
| 1 | Bran[b] | Harland | 1.04 | | 737 |
| 1 | Bran[g] | McCance | 1.105 | 1.20 | 1143 |
| | See also refs. 740–742,772 for other data on soft white and hard red wheat brans | | | | |
| 1 | Bran[b] | Inositol | 0.949 | | 785 |
| 1 | Bran | CZE | 2.964 | | 700 |
| 1 | Bran | Mössbauer | + | | 816 |
| 1 | Root | SEM/EMX | + | | 891 |
| 1 | Pollen | PE | 0 | 0.43 | 788 |
| *T. aestivum* × *Secale cereale* (× *Triticosecale* Wittm.) (Triticale) | | | | | |
| 12 | Whole grain | McCance | 0.137-0.531 | 0.57-1.00 | 1144 |
| 12 | –, flour | McCance | 0.052-0.188 | 0.16-0.29 | 1144 |
| 12 | –, bran | McCance | 0.057-0.219 | 0.74-1.08 | 1144 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| 13 | Whole grain | McCance | 0.075-0.118 | | 1145 |
| 13 | –, flour | McCance | 0.041-0.068 | | 1145 |
| 13 | –, bran | McCance | 0.023-0.095 | | 1145 |
| 5 | Seed | Harland | 0.28-0.33 | | 1146 |
| 1 | Grain[b] | HPLC | 0.28 | | 774 |
| See also ref. 1147 for various *Triticale* × *Agropyron* crosses | | | | | |
| *Triticum compactum* Host. (Club Wheat) | | | | | |
| 1 | Seed | GFC, PE | + | | 1138 |
| *Triticum durum* Desf. (Durum Wheat) | | | | | |
| 6 | Whole kernel[b] | McCance | 0.25-0.40 | | 1148 |
| 6 | –, bran[b] | McCance | 0.65-1.22 | | 1148 |
| 1 | Seed germ[b,c] | McCance | 0.597 | 1.244 | 1149 |
| 6 | Seed flour[b] | McCance | 0.13-0.20 | | 1148 |
| 6 | Semolina[b] | McCance | 0.04-0.10 | | 1148 |
| 1 | Seed protein body | Morton | 0.68 | 0.75 | 805 |
| 1 | Waldron bran[b] | McCance | 1.31 | | 749 |
| 1 | Bran[c] | HPLC | 0.79 | | 740 |
| *Triticum monococcum* L. (Einkorn) | | | | | |
| 1 | Seed | Harland | fig. | 0.640 | 830 |
| *Triticum spelta* L. (Spelt) | | | | | |
| 1 | Whole seed meal | McCance | 0.29 | 0.48 | 1150 |
| 1 | Unripe seed | McCance | 0.27 | | 1151 |
| *Triticum turgidum* L. (Poulard Wheat) | | | | | |
| 6 | Seed | Harland | fig. | 0.470-0.610 | 830 |
| *Vaccaria segetalis* (Neck.) Garcke (Cow Herb) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.36 | | 796 |
| *Vallisneria* spp. (Eelgrass) | | | | | |
| 1 | Whole plant | Harland | 0.0056 | 0.130 | 912 |
| *Vernonia amygdalina* Delile (Bitter Leaf) | | | | | |
| 1 | Leaf and stem | McCance | 0.018 | 0.240 | 837 |
| 1 | Leaf | McCance | 0.061 | 0.7 | 909 |
| *Vernonia galamensis* (Cass.) Less. (Ironweed) | | | | | |
| 1 | Defatted seed meal[c] | Harland | 0.716 | 64.4 (*sic*) | 1152 |
| *Vicia faba* L. (Broad (Faba) Bean) | | | | | |
| 23 | Whole bean | McCance | 0.21-0.47 | 0.405-0.894 | 1153 |
| 5 | Seed, cotyledon | McCance | 0.49-0.53 | | 1154 |
| 7 | Bean | McCance | 0.13-0.21 | | 1155 |
| 5 | Bean | McCance | 0.39-0.42 | 0.315-0.384 | 919 |
| 2 | Decoated seed | McCance | 0.089-0.290 | 0.394-0.786 | 1156 |
| 2 | Seed coat | McCance | 0.010-0.040 | 0.031-0.073 | 1156 |
| 1 | Mature seed | PC | + | | 810 |
| 1 | –, immature seed | PC | + | | 810 |
| 1 | Seed aleurone grain | McCance | 0.89 | 1.4 | 812 |
| 1 | Seed aleurone grain | PC | + | 1.4 | 812 |
| 1 | Seed protein fraction | McCance | 1.18 | | 1088 |
| 1 | Seed starch fraction | McCance | 0.25 | | 1088 |
| 1 | Defatted seed powder | Michel | 0.5275 | | 758 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| 4 | Whole seed | Harland | 0.20-0.32 | | 1091 |
| 2 | –, dehulled | Harland | 0.27-0.33 | | 1091 |
| 2 | –, hull | Harland | 0.017-0.056 | | 1091 |
| 2 | –, protein concentrate | Harland | 0.58-0.59 | | 1091 |
| 1 | –, protein isolate | Harland | 0.68 | | 1091 |
| 2 | Seed | HPLC | 0.097-0.172 | | 922 |
| 1 | Seed flour | Harland | 0.103 | | 926 |
| 1 | –, protein fraction | Harland | 0.243 | | 926 |
| 1 | –, starch fraction | Harland | 0.045 | | 926 |
| 1 | Seed, axis | $^{31}$P NMR | 0.422 | 0.728 | 824 |
| 1 | –, cotyledon | $^{31}$P NMR | 0.336 | 0.400 | 824 |
| 1 | Seed cotyledon | TEM/EDX | + | | 823 |
| 2 | Sprout | McCance | 0.202-0.203 | 0.416-0.518 | 1018 |
| *Vicia faba* L. ssp. *minor* L. (Small Horsebean) | | | | | |
| 1 | Bean | Undisclosed | 0.402 | | 1157 |
| 1 | Germinated bean | Undisclosed | 0.486 | | 1157 |
| *Vigna aconitifolia* (Jacq.) Mar. (Moth Bean) | | | | | |
| 1 | Seed | MCance | 0.32 | 0.45 | 1158 |
| 1 | Seed flour | McCance | 0.210 | 0.340 | 1159 |
| 4 | Whole seed | McCance | 0.240-0.253 | | 1160 |
| 4 | 60-h sprout | McCance | 0.108-0.129 | | 1160 |
| *Vigna ambacensis* Welw. ex Baker | | | | | |
| 3 | Seed | Harland | 0.121-0.200 | | 1161 |
| *Vigna angularis* (Willd.) Ohwi and Ohashi (Adzuki Bean) | | | | | |
| 1 | Seed | McCance | 0.042 | | 1162 |
| *Vigna catjang* (Burm. f.) Walp. (Catjang) | | | | | |
| 1 | Bean | McCance | 0.167 | 0.447 | 827 |
| *Vigna luteola* (Jacq.) Benth. (Hairypod Cowpea) | | | | | |
| 3 | Seed | Harland | 0.187-0.269 | | 1161 |
| *Vigna mungo* (L.) Hepper (Black Gram) | | | | | |
| 6 | Whole seed | McCance | 0.203 ± 0.009 | 0.415 ± 0.027 | 898 |
| 6 | –, decorticated | McCance | 0.228 ± 0.004 | 0.455 ± 0.011 | 898 |
| 4 | Whole seed | McCance | 0.182-0.188 | | 920 |
| 1 | Seed meal | McCance | 0.48 | 0.54 | 1163 |
| 1 | –, whey | McCance | 0.30 | | 1163 |
| 1 | Defatted seed | McCance | 0.17 | | 1164 |
| 4 | 48-h sprout | McCance | 0.102-0.115 | | 920 |
| *Vigna oblongifolia* A. Rich. | | | | | |
| 3 | Seed | Harland | 0.240-0.414 | | 1161 |
| *Vigna racemosa* G. Don | | | | | |
| 3 | Seed | Harland | 0.174-0.242 | | 1161 |
| *Vigna radiata* (L.) Wilcz. (Mung Bean) | | | | | |
| 5 | Whole seed | McCance | 0.311 ± 0.018 | 0.464 ± 0.005 | 898 |
| 5 | –, decorticated | McCance | 0.347 ± 0.005 | 0.489 ± 0.008 | 898 |
| 1 | Seed | McCance | 0.188-0.203 | 0.410 | 1051 |
| 1 | Defatted seed | McCance | 0.18 | | 1164 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| 1 | Bean | Harland | 0.177 | 0.376 | 925 |
| 1 | Bean | TLC, TLE | + | | 693 |
| 1 | Seed flour | Harland | 0.144 | | 926 |
| 1 | –, protein fraction | Harland | 0.404 | | 926 |
| 1 | –, starch fraction | Harland | 0.044 | | 926 |
| 1 | Sprout | McCance | 0.161 | 0.540 | 1051 |
| *V. radiata* × *V. mungo* | | | | | |
| 4 | Seed | McCance | 0.196-0.211 | | 1165 |
| *Vigna reticulata* Hook. f. | | | | | |
| 3 | Seed | Harland | 0.134-0.457 | | 1161 |
| *Vigna sesquipedalis* (L.) Fruw. (Yard Long Bean) | | | | | |
| 1 | Seed | McCance | 0.072 | 0.135 | 832 |
| 1 | Green pod | McCance | 0.034 | 0.045 | 832 |
| *Vigna subterranea* (L.) Verdc. (Bambara Groundnut) | | | | | |
| 1 | Seed | McCance | 0.083 | | 901 |
| 1 | Boiled bean | Harland | 0.197 | | 822 |
| 1 | 3-day sprout | McCance | 0.064 | | 901 |
| *Vigna umbellata* (Thunb.) Ohwi and Ohashi (Rice Bean) | | | | | |
| 5 | Whole bean | McCance | 0.528-0.639 | 0.234-0.249 | 1166 |
| 5 | –, defatted | McCance | 0.10-0.14 | | 1164 |
| 1 | Sprout | McCance | 0.120 | 0.400 | 1167 |
| *Vigna unguiculata* (L.) Walp. (Cowpea) | | | | | |
| 15 | Seed | McCance | 0.452-0.706 | | 1168 |
| 13 | Seed | Harland | 0.14-0.29 | | 1169 |
| 13 | Pea | McCance | 0.079-0.223 | 0.382-0.473 | 1170 |
| 10 | Whole bean | McCance | 0.079-0.093 | | 1171 |
| 4 | Whole seed | McCance | 0.28-0.39 | | 1172 |
| 4 | –, dehulled | McCance | 0.28-0.39 | | 1172 |
| 1 | Defatted bean | McCance | 0.14 | | 1164 |
| 1 | Seed flour | Harland | 0.214 | | 926 |
| 1 | –, protein fraction | Harland | 0.460 | | 926 |
| 1 | –, starch fraction | Harland | 0.070 | | 926 |
| 1 | Seed flour | HPLC | 0.156 | | 769 |
| 1 | Seed, axis | $^{31}$P NMR | 0.187 | 0.538 | 824 |
| 1 | –, cotyledon | $^{31}$P NMR | 0.301 | 0.360 | 824 |
| 1 | Young pod | McCance | 0.016 | 0.067 | 832 |
| 10 | 3-day sprout | McCance | 0.040-0.050 | | 1171 |
| 3 | 3-day sprout | McCance | 0.10-0.12 | 0.29-0.37 | 980 |
| *Vigna unguiculata* ssp. *dekindtiana* (Harms.) Verdc. | | | | | |
| 4 | Seed | Harland | 0.175-0.429 | | 1161 |
| *Vigna vexillata* (L.) A. Rich. (Zombi Pea) | | | | | |
| 5 | Seed | Harland | 0.185-0.428 | | 1161 |
| *Vigna vexillata* ssp. *macrosperma* | | | | | |
| 3 | Seed | Harland | 0.183-0.384 | | 1161 |
| *Vinca erecta* Regel and Schmalh. (Periwinkle) | | | | | |
| 1 | Defatted seed meal | Mukhamedova | 0.01 | | 796 |

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| *Viscum album* L. (Mistletoe) | | | | | |
| 1 | Shoot | McCance | 0.39-0.43 | | 1173 |
| 1 | Fat-free leaf flour[b,c] | Michel | 0.110 | | 757 |
| *Vitex doniana* (Sweet) | | | | | |
| 1 | Seed | McCance | 0.177 | | 828 |
| *Vitis vinifera* L. (Wine Grape) | | | | | |
| 1 | Seed | Harland | 0.06 | | 761 |
| *Voandzeia poissonii* A. Chev. (Dougoufoulo) | | | | | |
| 1 | Nut[b,c] | Undisclosed | + | | 1002 |
| *Washingtonia filifera* (Lindl.) Wendl. (California Fan-Palm) | | | | | |
| 1 | Seed endosperm | Microscopy | + | | 1174 |
| 1 | Seed endosperm | SEM | + | | 1174 |
| 1 | Seed endosperm | TEM/EDX | + | | 1174 |
| 1 | Haustoria | Microscopy | + | | 1074 |
| 1 | Haustoria | TEM/EDX | + | | 1074 |
| *Wolffiella floridana* (Sm.) Thomps. (Water Meal) | | | | | |
| 1 | Whole plant | PE | + | | 695 |
| *Xanthosoma mafaffa* (L.) Schott. (Lime Zinger) | | | | | |
| 1 | Leaf | McCance | 0.037 | 0.017 | 963 |
| *Xanthosoma sagittifolium* (L.) Schott. (Tannia) | | | | | |
| 1 | Leaf | McCance | 0.048 | 1.3 | 909 |
| *Xanthosoma* spp. (Cocoyam) | | | | | |
| 1 | Boiled leaf | Harland | 0.005 | | 955 |
| 1 | Boiled root | Harland | 0.010 | | 955 |
| *Xylia xylocarpa* (Roxb.) Theob. (Burma Pyingado) | | | | | |
| 1 | Seed flour | McCance | 0.102 | 0.342 | 1175 |
| *Xylomelum angustifolium* Kipp. | | | | | |
| 1 | Seed cotyledon | Microscopy | + | | 877 |
| 1 | Seed cotyledon | SEM/EMX | + | | 877 |
| *Xylopia aethiopica* (Dun.) A.Rich. (Guinea Pepper) | | | | | |
| 1 | Seed | McCance | 0.149 | | 828 |
| *Zantedeschia aethiopica* (L.) Spreng. (Calla Lily) | | | | | |
| 1 | Pollen | PE | 0.07 | 0.62 | 788 |
| *Zea mays* L. (Corn) | | | | | |
| 9 | Grain | McCance | 0.313-0.419 | | 736 |
| 2 | Yellow grain | McCance | 0.149-0.276 | 0.199-0.368 | 826 |
| 1 | –, meal | McCance | 0.277-0.314 | 0.364-0.407 | 826 |
| 1 | Mature seed | PC | + | | 810 |
| 1 | Seed germ, defatted | McCance | 1.35 | | 699 |
| 2 | Seed germ, defatted | DGE | + | | 699 |
| 1 | Seed flour[b] | McCance | 0.045 | 0.103 | 1176 |
| 1 | Whole kernel | McCance | 0.144-0.234 | 0.20-0.30 | 1177 |
| 1 | –, germ | McCance | 1.208-1.782 | 1.47-2.10 | 1177 |
| 1 | –, floury endosperm | McCance | 0.0244-0.0520 | 0.05-0.09 | 1177 |
| 1 | –, horny endosperm | McCance | 0.0031-0.0148 | 0.02-0.04 | 1177 |
| 1 | –, hull | McCance | 0.0053-0.0197 | 0.02-0.03 | 1177 |

[a]Percentage of total P; [b]Species unstated; [c]Basis not given; [d]Negligible (<1% of total P); [e]As is basis; [f]Fresh weight basis; [g]Air-dry basis; [h]Mean ± standard error; [i]Mixture; [j]See also ref. 1184.

*Continued*

**Table 2-4** Phytic Acid Content of Plants—cont'd

| No. | Plant part | Method | % P (phytate) | % P (total) | References |
|---|---|---|---|---|---|
| 1 | Seed, milky stage | McCance | 0.107 | 0.393 | 842 |
| 1 | High protein seed (65th to 81st generation) | McCance | | | 1178 |
| 1 | –, germ | McCance | 3.0 | 3.6 | 1178 |
| 1 | –, endosperm | McCance | 0.022 | 0.037 | 1178 |
| | | Also data for low protein seed (65th to 81st) and both (83rd) | | | |
| 2 | Seed gluten meal | McCance | 0.35-0.36 | 0.58 | 1179 |
| 1 | Degermed seed meal | McCance | 0.07 | 0.10 | 1179 |
| 1 | Seed zein | McCance | 0.00 | | 1141 |
| 1 | Defatted seed powder | Michel | 0.294 | | 758 |
| 2 | Grain | Harland | 0.193-0.207 | | 936 |
| 1 | Grain | CZE | 0.363 | | 700 |
| 1 | Whole seed, embryo | Microscopy | + | | 1180 |
| 1 | Seed flour, 65% extraction | Harland | 0.066 | | 822 |
| 1 | –, bran | Harland | 0.341 | | 822 |
| 1 | Whole grain[b] | HPLC | 0.30 | | 774 |
| 2 | –, bran[b] | HPLC | 0.01-0.02 | | 774 |
| 1 | Seed bran[b] | McCance | 0 | | 740 |
| 1 | Whole seed meal[b] | $^{31}$P NMR | 0.17 | | 743 |
| 1 | Bran[b,c] | $^{31}$P NMR | 0 | | 781 |
| 1 | Root | $^{31}$P NMR | n.d. | | 43 |
| 1 | Root | SEM/EMX | + | | 891 |
| 1 | Germinated seed | SEM/EMX | + | | 43 |
| 1 | Flower ovule | McCance | 0.013 | 0.608 | 1181 |
| 1 | Pollen | McCance | 0.043 | | 1181 |
| 1 | Silks | McCance | 0.017 | | 1181 |
| | | No phytic acid in stalks, leaves, tassels, shank, or cob. | | | 1182 |
| 1 | Pollen | PE | 0.07 | 0.53 | 788 |
| High lysine corn | | | | | |
| 1 | Grain[b,e] | McCance | 0.28 | | 1183 |
| 1 | Whole kernel[g] | McCance | 0.27 | 0.31 | 1178 |
| 1 | –, germ[g] | McCance | 1.61 | 1.78 | 1178 |
| 1 | –, endosperm[g] | McCance | 0.01 | 0.03 | 1178 |
| 1 | –, hull[g] | McCance | 0.07 | 0.10 | 1178 |
| *Zingiber officinale* Rosc. (Ginger) | | | | | |
| 1 | Root[e] | McCance | 0.0048 | 0.062 | 842 |

In this table, unlike most of the others in this book, the coverage for each entry is selective rather than comprehensive because of extensive duplication in the published literature. Preference is given to studies that report data for two or more varieties or cultivars, but for the remainder, the author has selected the one that in his opinion is the most reliable.

[a]Percentage of total P.
[b]Species unstated.
[c]Basis not given.
[d]Negligible (<1% of total P).
[e]As is basis.
[f]Fresh weight basis.
[g]Air-dry basis.
[h]Mean ± standard error.
[i]Mixture.
[j]See also ref. 1184.

# 3 Lower *myo*-Inositol Phosphates

This chapter covers the *myo*-inositol phosphates and their glyceryl esters with the exception of phytic acid, which is covered in Chapter 2, and of phosphatidylinositol (PI) and its derivatives, which are covered in Chapter 4. The following is a complete list of the compounds described in this chapter:

| $InsP_n$ | Inositol phosphate | Glyceryl ester |
|---|---|---|
| InsP | Ins(1)P, Ins(2)P, Ins(3)P, Ins(4)P | GroPIns |
| $InsP_2$ | Ins(1,2)$P_2$, Ins(1,4)$P_2$, Ins(3,4)$P_2$, Ins(4,5)$P_2$ | GroPIns(3)P, GroPIns(4)P |
| $InsP_3$ | Ins(1,2,3)$P_3$, Ins(1,2,6)$P_3$, Ins(1,4,5)$P_3$, Ins(1,5,6)$P_3$, Ins(3,4,6)$P_3$ | GroPIns(3,4)$P_2$, GroPInsP(4,5)$P_2$ |
| $InsP_4$ | Ins(1,2,3,6)$P_4$, Ins(1,2,5,6)$P_4$, Ins(1,3,4,5)$P_4$, Ins(1,4,5,6)$P_4$, Ins(3,4,5,6)$P_4$ | |
| $InsP_5$ | Ins(1,2,3,4,6)$P_5$, Ins(1,2,3,5,6)$P_5$, Ins(1,2,4,5,6)$P_5$, Ins(1,3,4,5,6)$P_5$ | |

The full names and structures of the lower *myo*-inositol phosphates are given in the introduction to each section. The nomenclature used here conforms to the recommendations of the Joint IUPAC-IUB Commission on the Nomenclature of Cyclitols issued in 1973.[1194] Caution should be exercised when reading older literature as the inositol ring numbering may be different and the sign (+ or −) may be reversed.

For general references on the subject of this chapter see Cosgrove and Irving,[676] Irvine,[1195] Morré *et al.*,[1196] or Biswas and Biswas.[1197]

## Occurrence

No *myo*-inositol phosphate with fewer than six phosphate groups can be detected in rice or wheat seedlings during the first 14 days of germination, during which *myo*-inositol and inorganic phosphate are released and the phytate content falls to zero.[1187,1198] Short-term feeding experiments with [$^3$H]-*myo*-inositol or $^{32}P_i$ produced InsP and phytate but no other intermediates.[1187] Many of the lower *myo*-inositol phosphates reported in Table 3-4 may be artifacts of the hydrolysis of phytic acid by endogenous phytase[1208] or by chemical reagents during the course of extraction, isolation, and analysis.

## Synthesis

The *myo*-inositol phosphates ($InsP_1$ through $InsP_6$) may be prepared (a) by phosphorylation of *myo*-inositol with polyphosphoric acid[714] or ATP,[1209] (b) by acid- or base-catalyzed hydrolysis of phytic acid,[721] or (c) by enzymatic hydrolysis of phytic acid with 3-phytase


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[E.C. 3.1.3.8], 6-phytase [E.C. 3.1.3.26],[1210] or acid phosphatase [E.C. 3.1.3.2].[1210] The polyphosphates are readily separated by ion exchange chromatography.

## Hydrolysis

Hydrolysis of phytic acid ($InsP_6$) *in vitro* with acid, base, or enzyme catalysts produces a mixture of *myo*-inositol polyphosphates whose relative proportions change during the course of the reaction. The polyphosphates are readily separated into pentakis-, tetrakis-, tris-, bis-, and monophosphate fractions by chromatography or electrophoresis. Each fraction can (and often does) contain more than one stereoisomer (Table 3-1).

**Table 3-1** Isomer Distribution in *myo*-Inositol Polyphosphates

| | Maximum number of isomers | | | | Hydrolysis of phytic acid by phytase | | |
|---|---|---|---|---|---|---|---|
| $InsP_n$ | D | L | Meso | Total | $[\alpha]_D$[a] | $K_M \times 10^{-3}$[a] | $P_{50}$[b] |
| $InsP_5$ | 2 | 2 | 2 | 6 | n.d. | 1.7 | – |
| $InsP_4$ | 6 | 6 | 3 | 15 | −4.09 | 5.0 | 17.8 |
| $InsP_3$ | 8 | 8 | 4 | 20 | −8.26 | 4.4 | 16.8 |
| $InsP_2$ | 6 | 6 | 3 | 15 | −5.95 | 1.2 | 15.4 |
| $InsP_1$ | 2 | 2 | 2 | 6 | 0 | 1.5 | – |

[a]Posternak and Posternak.[1211]
[b]Percentage of total P at 50% hydrolysis.[1212]

*In vitro* hydrolysis of phytic acid by wheat bran phytase at pH 5.2 and 55 °C produces a mixture of polyphosphates whose middle fractions—$InsP_4$, $InsP_3$, and $InsP_2$—are optically active (Table 3-1).[723,1211] The initial rates of hydrolysis and activation energy (11 kcal/mol) of each fraction are nearly the same, even though the more highly phosphorylated members are attacked preferentially.[1212] The heats of hydrolysis of the pentakis-, tetrakis-, and trisphosphates are not significantly different ($\Delta H_{app}$ −2820 to −3040 cal/mol $P_i$), but that of the bisphosphate is higher (∼4000 cal/mol $P_i$).[1213]

Phytic acid is scarcely attacked by acids or bases at temperatures below 100 °C. In aqueous solution at 100 °C, the rate of hydrolysis is negligible at pH 12, rises to a maximum at pH 4, falls to a minimum at pH −1, and then rises steeply with increasing acidity.[1214] This behavior is typical of monoalkyl esters of phosphoric acid.

Hydrolysis at pH 4, monitored by PC,[692] PE,[698] or IEC,[719] produces a mixture of polyphosphates whose distribution changes from pentakis- to monophosphate with time of heating. Prolonged hydrolysis at pH 9 yields mainly the tetrakis- and trisphosphates.[721] If the pH is not allowed to fall below 7.5, the monophosphate Ins(2)P is obtained in 55% yield after 60 h of refluxing.[1215] For accumulation of the tris- and bisphosphates, autoclaving at 120 °C is more efficient than enzymatic hydrolysis.[1210]

## Extraction

The inositol polyphosphates are usually extracted from plant tissues with ice-cold 0.5*M* perchloric acid or trichloroacetic acid. After extraction, it is good practice to remove the excess acid promptly by neutralization with KOH to precipitate the perchloric acid

as its highly insoluble potassium salt[1216] or by extraction with ether to remove the trichloroacetic acid.[950] Other extractants that have been employed are 2*N* formic acid,[1217] 0.4*N* HCl,[1218] and phenol.[683] If the plant tissue is to be monitored for phosphatidylinositol (PI), it may be extracted with $CHCl_3$/methanol/3*N* HCl (6:6:1) and the extracts analyzed separately for PI (organic phase) and InsPs (aqueous phase).[1219,1220] In one case *n*-$Bu_4NHSO_4$ was used in place of HCl.[1221]

## Separation and Analysis

### *(1) Precipitation Method*

Before the advent of chromatography, the inositol polyphosphates were separated from each other by selective precipitation as barium salts whose solubility increases in the order $InsP_5$ (and $InsP_6$) > $InsP_4$ > $InsP_3$ > $InsP_2$ and $InsP_1$. The barium inositol monophosphates are water soluble.[1211,1222] This method is still employed occasionally in conjunction with other methods of isolation.

### *(2) Chromatographic Methods*

The use of chromatographic methods to separate the *myo*-inositol polyphosphates into fractions of equal phosphorus content is illustrated in Table 3-2. $InsP_6$ and $InsP_5$ are poorly separated with solvents or buffers of pH 3.6 or above[692,698] but can be separated by lowering the pH to 1.5.[787,1226] Paper chromatography (PC) and paper electrophoresis (PE) have been employed much more often than thin-layer methods (TLC or TLE) for qualitative identification of InsP fractions. Gel filtration chromatography (GFC) is not as useful. The InsP spots are usually detected by spraying the paper or thin-layer plate with the Hanes/Isherwood reagent followed by UV exposure to improve color development; this treatment hydrolyzes the InsPs leaving blue spots (phosphomolybdate) on a white background.[35]

Ion exchange chromatography (IEC) is the method of choice for either analytical or preparative resolution of InsP mixtures. In early work, Dowex 2 ($Cl^-$) resin was employed, but

**Table 3-2** Chromatography of *myo*-Inositol Polyphosphates

| Fraction | PC[a] | TLC[b] | PE[c,d] | TLE[d,e] | GFC[f] | HPLC[g] |
|---|---|---|---|---|---|---|
| $InsP_6$ | 0.09 | 1.00 | 2.05 | 1.68 | 0.19 | 58 |
| $InsP_5$ | 0.10 | 1.22 | 1.95 | 1.60 | 0.19 | 53.8 |
| $InsP_4$ | 0.17 | 1.32 | | 1.47 | 0.25 | 48.9 |
| $InsP_3$ | 0.22 | | 1.45 | 1.30 | 0.33 | 43.1 |
| $InsP_2$ | 0.27 | | 1.20 | 1.10 | 0.44 | 36.4 |
| $InsP_1$ | 0.38 | | 0.92 | 0.86 | 0.59 | 27 |

[a] $R_f$ in *n*-PrOH/$NH_3$/$H_2O$ (5:4:1).[692]

[b] Travel relative to phytic acid = 1.00 on silica gel H after methylation with diazomethane and elution with methanol.[1223]

[c] 800 V, 0.1*M* oxalate buffer, pH 1.5, 0 °C.[1224]

[d] Travel relative to picric acid = 1.00.

[e] 1000 V, 0.1*M* oxalate buffer, pH 1.5.[693]

[f] Distribution coefficient $K_D$ on Sephadex G-25, 0.2*M* LiCl.[1225]

[g] Elution time (min.) on Aminex A-27 with a 0.10*M* → 0.50*M* NaCl gradient.[767]

Dowex 1 ($Cl^-$ or $HCO_2^-$) is now preferred. The InsPs are eluted in the order $InsP_1 \rightarrow InsP_6$ with gradients of HCl[721] or LiCl.[723] In some cases, the $InsP_2$, $InsP_3$, $InsP_4$, or $InsP_5$ fractions split into two or more discrete peaks owing to differences in elution behavior between the isomers.[719,1210,1227] The lower InsPs ($InsP_1$ to $InsP_3$) are often eluted from Dowex 1 ($HCO_3^-$) with an ammonium formate gradient followed by an HCl gradient for the higher InsPs.

Since 1985, high-performance liquid chromatography (HPLC) methods have been developed for separating the *myo*-inositol polyphosphates into fractions of different phosphorus content. Many of these methods employ strong (Partisil SAX, Aminex A-27, Mono Q) or weak (IC-PAK-A) anion exchange stationary phases, and mobile phases similar to those of conventional IEC. Separation of a partial hydrolyzate of phytic acid into six fractions on Aminex A-27 (Bio-Rad) with a $0.1M \rightarrow 0.5M$ linear NaCl gradient at pH 10 is shown in Table 3-2.[767] Some HPLC methods are powerful enough to separate the InsP fractions into their individual isomers.[1228]

One such method is gradient ion chromatography (IC) using a Dionex AS3 column installed in the HPLC unit.[1229]

## Analysis Without Separation

### *(3) Protein-Binding Assay (PBA) Method*

Intense interest in D-*myo*-inositol 1,4,5-trisphosphate as a calcium stimulant in animal cells prompted the development of the PBA method, which is specific for this compound. Similar in principle to the Gilman protein-binding assay for c-AMP described in Chapter 5, page 375, the PBA method employs a binding protein of bovine origin and 2-[$^3$H]Ins(1,4,5)$P_3$ as the tracer. All the data given in Table 3-3 were obtained using commercial kits available from Amersham, UK.

> *Ins(1,4,5)$P_3$ levels in [wheat] root tissues were determined using an $IP_3$ assay kit (TRK 1000; Amersham; Toyoda et al., 1993; Challis, 1995). Briefly, root tips were frozen in liquid $N_2$ and then ground in 0.5 mL of 20% perchloric acid at 4 °C for 5 min; the samples were then centrifuged at 2000*g *for 15 min. The supernatant was then neutralized with 1.5 M KOH–60 mM Hepes, and the precipitated $KClO_4$ was removed by centrifugation (2000*g*, 15 min). Aliquots of the supernatant were used for analysis of $IP_3$ as described in the assay kit.*
>
> Jones, D. L.; Kochian, L. V., "Aluminum Inhibition of the Inositol 1,4,5-Trisphosphate Signal Transduction Pathway in Wheat Roots: A Role in Aluminum Toxicity?", *Plant Cell* **1995**, *7*(11), 1913–1922,[1235] reprinted by permission of the American Society of Plant Biologists, © 1995.

### *(4) Other Methods*

Johnson *et al.*[689] have described a method whereby the major components of a complex mixture, such as a partial phytic acid hydrolyzate, can be analyzed without prior separation. The method uses total correlation spectroscopy (TOCSY) to identify the $^1$H NMR resonance of the six *myo*-inositol hydrogens in each component.

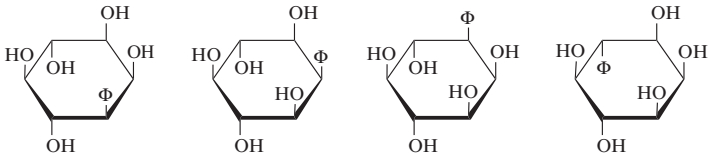
**Table 3-3** D-Ins(1,4,5)$P_3$ in Plants by the PBA Method*

| No. | Plant part | Ins(1,4,5)$P_3$ | References |
|---|---|---|---|
| *Beta vulgaris* L. (Red beet) | | | |
| 1 | Tuber | 0.0088 | 1230 |
| *Lycopersicon esculentum* Mill. (Tomato) | | | |
| 1 | Seedling, root | 3.550 | 1231 |
| 1 | –, cotyledon | 0.275 | 1231 |
| 1 | –, epicotyl | 0.180 | 1231 |
| *Medicago sativa* L. (Lucerne) | | | |
| 1 | Cell suspension culture | 0.030 | 1232 |
| *Papaver rhoeas* L. (Corn Poppy) | | | |
| 1 | Pollen | 0.5 | 1233 |
| *Pisum sativum* L. (Peas) | | | |
| 1 | Plasma membrane[a] | 0.8 | 1234 |
| 1 | Epicotyl | 0.013 | 1234 |
| *Triticum aestivum* L. (Wheat) | | | |
| 1 | Root | 0.4 | 1235 |
| *Zea mays* L. (Maize) | | | |
| 1 | Seedling, root | 0.23 | 1236 |
| 1 | Coleoptile | 0.82 | 1236 |

*nmol/g fresh weight basis unless stated otherwise.
[a]nmol/mg protein.

## *myo*-Inositol Monophosphates

There are six *myo*-inositol monophosphates, of which four are important plant metabolites ($\Phi = OP(O)(OH)_2$) (Fig. 3-1):




D-*myo*-Inositol 1-Phosphate (Ins(1)P), $C_6H_{13}O_9P$; Beilstein **6**, $E_{III}$ 6931-6932. D-*(or 1D)-myo-Inositol 1-(Dihydrogen Phosphate)* [1959].

*myo*-Inositol 2-Phosphate (Ins(2)P), $C_6H_{13}O_9P$; Beilstein **6**, $E_I$ 590, $E_{II}$ 1159, $E_{III}$ 6932, $E_{IV}$ 7925. *myo-Inositol 2-(Dihydrogen Phosphate)* [1914].

D-*myo*-Inositol 3-Phosphate (Ins(3)P), $C_6H_{13}O_9P$; Beilstein **6**, $E_{III}$ 6931. D-*myo-Inositol 3-(Dihydrogen Phosphate)* [1960].

D-*myo*-Inositol 4-Phosphate (Ins(4)P), $C_6H_{13}O_9P$; Beilstein **6**, $E_{III}$ 6932. D-*myo-Inositol 4-(Dihydrogen Phosphate)* [1961].

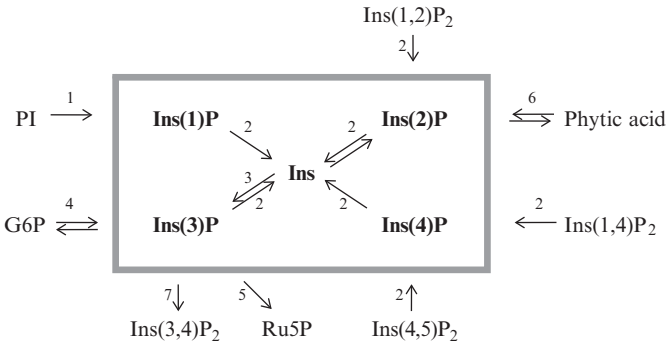



**FIGURE 3-1** ***myo*-Inositol Monophosphates**. (1) PI phospholipase C [E.C. 3.1.4.10]. (2) InsP phosphatase [E.C. 3.1.3.25], Mg(II). (3) Ins(3)P kinase [E.C. 2.7.1.64], ATP, Mg(II).[1237] (4) Ins(3)P synthase [E.C. 5.5.1.4], NAD.[1237] (5) Ins(3)P dehydrogenase, NAD. (6) 6-Phytase [E.C. 3.1.3.26]. (7) Phytate synthase.[1238]

## Occurrence

Ins(1)P has been identified in carrot,[950] lucerne,[1239] tobacco,[1200] and Madagascar periwinkle[1200] cell suspension cultures, in apple buds,[1240] in pea flour,[1241] in trumpet lily pollen,[1217] and in rain tree pulvini.[1219] Ins(2)P occurs in rice,[1186] tobacco,[1200] and Madagascar periwinkle[1200] cell suspension cultures, in wheat ear stalks,[1242] and in ripening rice grain.[1242] Ins(3)P has been identified in barley aleurone tissue[1208] and in giant duckweed.[1243] Ins(4)P occurs in tobacco and Madagascar periwinkle cell suspension cultures,[1200] in cauliflower hypocotyl,[1244] and in pea flour.[1241]

## Physical Properties

### D-*myo*-Inositol 1-Phosphate

Ins(1)P [R.N. 15421-51-9]: $[\alpha]_D^{25}$ −9.8° ($H_2O$)[1245]; p$K_a$ 6.16 (potentiometric),[1246] 6.08 ($^{31}$P NMR).[68] Spectra: ORD,[1247] $^{31}$P NMR.[68] Chromatography: PC,[1245] TLC,[813] IEC,[1248] GC,[1249] HPLC,[1250] IC,[107] LC/MS.[1251] Electrophoresis: PE.[1239] Additional data for DL-Ins(1)P: p$K_a$ 6.50,[1252] $^1$H NMR (fig.),[687,1253] $^{13}$C NMR (fig.),[1253] $^{31}$P NMR (fig.),[1252] HPTLC,[407] capillary electrophoresis.[1254]

$(C_6H_{11}NH_2)_3C_6H_{13}O_9P$: Needles,[1255] mp 197-209 °C (variable),[1245] $[\alpha]_D^{25}$ +3.4° ($H_2O$),[1245] $[M]_D$ +8.8° (calc.).[1256] Spectra: IR (fig.),[1257] ORD (fig.),[1257] $^1$H NMR,[1255] $^{13}$C and $^{31}$P NMR,[1258] MS (FAB),[1259] MS/MS (FAB, fig.).[1260] Chromatography: PC.[1257]

### *myo*-Inositol 2-Phosphate

Ins(2)P [R.N. 7336-80-3]: Large colorless prisms[1222] or hexagonal plates[1261] with a sharp, somewhat astringent taste, mp 201-202 °C dec., $[\alpha]_D$ 0° ($H_2O$), very sol. $H_2O$, insol. organic solvents[1222]; p$K_a$ 1.21, 5.73 (potentiometric),[1215] 5.83 ($^{31}$P NMR),[1252] *ab initio* calculations (HF/6-31G* method).[1262] Spectra: IR (fig.),[1263] $^1$H NMR,[687,1264] 2d-$^1$H NMR (fig.),[689] $^{13}$C NMR (fig.),[1253] $^{31}$P NMR,[68] MS (FAB),[690] ORD.[1242] Chromatography: PC,[1265] TLC,[1266] IEC,[1267] cellulose powder,[1265] HPLC,[1268] IC,[107]

GC,[1269] GC/MS (EI,CI),[690] LC/MS.[1251] Electrophoresis: PE,[1239] capillary,[1254] CZE/MS.[1270] *Monohydrate* [R.N. 54275-72-8]: White acicular monoclinic crystals, mp ≅ 190 °C dec., d 1.791; conformation $1_{ax}(C^2)/5_{eq}$, X-ray.[1271]
$Na_2C_6H_{11}O_9P$: Fine white amorphous powder, slightly hygroscopic.[1261]
$BaC_6H_{11}O_9P$: Amorphous solid, sol. $H_2O$.[1261] Tetrahydrate.[1211] Other salts are water soluble except for the lead salt.[1222]
$(C_6H_{11}NH_2)C_6H_{13}O_9P{\cdot}H_2O$: Needles, mp 203-205 °C.[722]
$(C_6H_{11}NH_2)_2C_6H_{13}O_9P{\cdot}4H_2O$: Rosettes of needles, mp 211-213 °C.[722] Spectra: IR,[1245] MS(FAB),[690] MS/MS (FAB, fig.),[1260] X-ray (powder photo).[722] Chromatography: PC.[1245]
$(C_{23}H_{26}N_2O_4)C_6H_{13}O_9P{\cdot}1.5H_2O$ (brucine salt): Crystalline, mp 244-247 °C.[722]

D-*myo*-Inositol 3-Phosphate

Ins(3)P [R.N. 2831-74-5]: $[\alpha]_D^{25}$ +9.3° ($H_2O$).[1272] Spectra: $^1H$ NMR (fig.).[1264] Chromatography: PC,[1272] column,[1265] HPLC,[1268] GC,[1249] GC/MS (EI,CI).[690]
$(C_6H_{11}NH_2)_2C_6H_{13}O_9P$: Needles, mp 190-192 °C,[1273] $[\alpha]_D^{25}$ −3.2° ($H_2O$).[1272] Spectra: IR,[1272] MS (FAB).[1259]

D-*myo*-Inositol 4-Phosphate

Ins(4)P [R.N. 69256-52-6]: Spectra: GC/MS (EI,CI).[690] Chromatography: PC,[1274] IEC,[1274] HPLC.[1268]
$(C_6H_{11}NH_2)_2C_6H_{13}O_9P{\cdot}1.5H_2O$: Crystals, mp 183-188 °C dec.,[1259] $[\alpha]_D^{25}$ −1.3° ($H_2O$).[1274] Spectra: IR,[1274] $^1H$ NMR,[1259] $^{13}C$ NMR,[1259] $^{31}P$ NMR,[1259] MS (FAB).[1259] Chromatography: HPLC.[1275]

## Synthesis

Ins(1)P may be prepared (a) by phosphorylation of D-2,3,4,5,6-penta-*O*-benzyl-*myo*-inositol with diphenyl phosphorochloridate,[1257] of D-2,3,4,5,6-penta-*O*-benzoyl-*myo*-inositol with *o*-xylene-α,α-diyl *N*,*N*-diethylphosphoramidite,[1255] of 4,6-dibenzyl-1,2-*O*-isopropylidene-5-tetrahydro-2*H*-pyran-2-yl-1L-*myo*-inositol with 2-diethylamino-1,3,2-benzodioxaphosphepane,[1258] or of D-2,3,4,5,6-penta-*O*-acetyl-*myo*-inositol with $POCl_3$ and benzyl alcohol,[1276] or (b) by hydrolysis of soybean phosphatidylinositol with 2*N* KOH.[1245]

Ins(2)P may be prepared (a) by phosphorylation of 1,3,4,5,6-penta-*O*-acetyl-*myo*-inositol with diphenyl phosphorochloridate[1261] or of 4,6-di-*O*-benzyl-*myo*-inositol orthoformate with tetrabenzyl pyrophosphate,[1277] (b) by hydrolysis of phytic acid with wheat bran phytase [E.C. 3.1.3.26],[1278] or (c) by prolonged heating of phytic acid in aqueous solution at pH 7.5 and 100 °C.[1215]

Ins(3)P may be prepared (a) by phosphorylation of D-1,2,4,5,6-penta-*O*-benzyl (or *O*-benzoyl)-*myo*-inositol with diphenyl phosphorochloridate[1272,1273] or of D-1,2,4,5,6-penta-*O*-acetyl-*myo*-inositol with $POCl_3$ and benzyl alcohol[1276] or (b) by the action of Ins(3)P synthase [E.C. 5.5.1.4] on G6P in the presence of DPN.[1279]

Ins(4)P may be prepared by phosphorylation of D-3-*O*-benzyl-1,2:4,5-*O*-dicyclohexylidene-*myo*-inositol with diphenyl phosphorochloridate,[1275] of

D-2,3-*O*-camphanylidene-5,6-*O*-isopropylidene-*myo*-inositol with 2-dimethylamino-5,6-benzo-1,3,2-dioxaphosphepane,[1259] or of 3-(1-(*S*)-camphanyl)-1,2:5,6-dicyclohexylidene-D-*myo*-inositol with dibenzyl *N*,*N*-diethylphosphoramidite.[1280]

### Hydrolysis

Ins(1)P and Ins(3)P are both hydrolyzed to *myo*-inositol and $P_i$ by yeast inositol 1-phosphatase [E.C. 3.1.3.27]. Their rates of hydrolysis at 29 °C and pH 7.7 are identical.[1279] Ins(2)P is hydrolyzed to *myo*-inositol and $P_i$ by 3% $H_2SO_4$ at 120-125 °C or by 10% $NH_4OH$ at 150 °C.[1222]

### Conformation

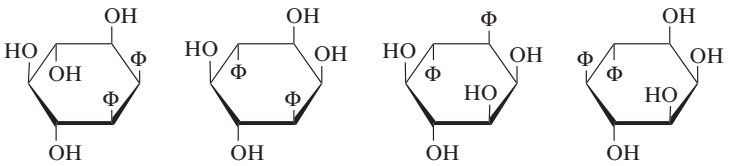
Ins(2)P adopts the $1_{ax}/5_{eq}$ conformation over the entire pH range 1.0-13.0, according to $^1H$ NMR analysis. There is no evidence for the $5_{ax}/1_{eq}$ form.[1281]

### Analytical Methods

Ins(1)P and Ins(3)P may be assayed by enzymatic hydrolysis with InsP phosphatase [E.C. 3.1.3.25] from rat testes; Ins(2)P does not interfere.[1282] Ins(2)P may be assayed by oxidation with periodic acid and colorimetric measurement of the liberated $P_i$, but this method does not distinguish Ins(2)P from the other monophosphates.[4221]

## *myo*-Inositol Bisphosphates

There are 15 *myo*-inositol bisphosphates, of which 4 are important plant metabolites ($\Phi = OP(O)(OH)_2$):




**D-Ins(1,2)$P_2$** L-Ins(2,3)$P_2$ | **D-Ins(1,4)$P_2$** L-Ins(3,6)$P_2$ | **D-Ins(3,4)$P_2$** L-Ins(1,6)$P_2$ | **D-Ins(4,5)$P_2$** L-Ins(5,6)$P_2$

D-*myo*-Inositol 1,2-Bisphosphate (Ins(1,2)$P_2$), $C_6H_{14}O_{12}P_2$; Beilstein **6**, $E_{III}$ 6933. D-*myo-Inositol 1,2-Bis(Dihydrogen Phosphate)* [1962].

D-*myo*-Inositol 1,4-Bisphosphate (Ins(1,4)$P_2$), $C_6H_{14}O_{12}P_2$; unlisted in Beilstein. D-*myo-Inositol 1,4-Bis(Dihydrogen Phosphate)* [1961].

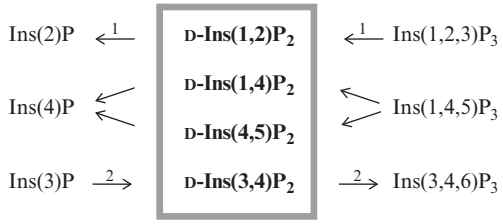



**FIGURE 3-2 *myo*-Inositol Bisphosphates**. (1) 6-Phytase [E.C. 3.1.3.26]. (2) Phytic acid synthase.[1238]

D-*myo*-Inositol 3,4-Bisphosphate ($Ins(3,4)P_2$), $C_6H_{14}O_{12}P_2$; unlisted in Beilstein. D-*myo-Inositol 3,4-Bis(Dihydrogen Phosphate)* [1996].

D-*myo*-Inositol 4,5-Bisphosphate ($Ins(4,5)P_2$), $C_6H_{14}O_{12}P_2$; Beilstein **6**, $E_{III}$ 6934. D-*myo-Inositol 4,5-Bis(Dihydrogen Phosphate)* [1961].

## Occurrence

$Ins(1,2)P_2$ has been identified only in barley aleurone tissue.[1208] $Ins(1,4)P_2$ occurs in barley aleurone tissue[1208] and mesophyll cells,[1283] in apple buds,[1240] in giant duckweed,[1243] in rain tree pulvini,[1219] in cauliflower hypocotyl,[1244] and in tobacco,[1200] Madagascar periwinkle[1200] and lucerne[1239] cell suspension cultures. $Ins(1,5)P_2$ has been reported in pea flour.[1241] $Ins(2,4)P_2$ has been reported in tobacco and Madagascar periwinkle cell suspension cultures[1200] and in pea flour.[1241] $Ins(3,4)P_2$ has been identified in giant duckweed.[1243] $Ins(4,5)P_2$ occurs in barley mesophyll cells (Fig. 3-2).[1283]

## Physical Properties

### D-*myo*-Inositol 1,2-Bisphosphate

$Ins(1,2)P_2$ [R.N. 23410-61-9]: $[\alpha]_D^{25}$ −4.4° ($H_2O$).[1284] PE,[723,1284] HPLC.[161] Additional data for DL-$Ins(1,2)P_2$ [R.N. 131321-70-5]: p$K_a$ 5.74, 7.97; microconstants for the first four dissociation equilibria.[1252] Spectra: 2d-$^1$H NMR,[687] $^{13}$C NMR,[1195] $^{31}$P NMR.[1285] Chromatography: IEC.[1227] Electrophoresis: CE,[1254] CZE/MS.[1270]

$Ba_2C_6H_{10}O_{12}P_2$: Slightly soluble in $H_2O$.[676]

$(NH_3)_4C_6H_{14}O_{12}P_2$: $[\alpha]_D^{25}$ −1.2° ($H_2O$).[1284]

$(C_6H_{11}NH_2)_4C_6H_{14}O_{12}P_2$: $[\alpha]_D^{25}$ −4.1° ($H_2O$).[723]

### D-*myo*-Inositol 1,4-Bisphosphate

$Ins(1,4)P_2$ [R.N. 74465-19-3]: Spectra: $^1$H NMR (fig.),[1264] $^{31}$P NMR,[1264] MS(FAB, fig.),[690] GC/MS.[690] Chromatography: IEC,[1248] HPLC,[1250] IC,[107] GC.[1269] Electrophoresis: PE.[1239] Additional data for DL-$Ins(1,4)P_2$ [R.N. 107494-29-1]: p$K_a$ 6.22, 6.59 (potentiometric).[1286] Spectra: 2d-$^1$H NMR,[687] $^{13}$C NMR.[1285]

$Ba_2C_6H_{10}O_{12}P_2$: Slightly soluble in $H_2O$.[676]

$(NH_3)_4C_6H_{14}O_{12}P_2$: Spectra: FAB-MS/MS (fig.).[1260]

$(C_6H_{11}NH_2)_4C_6H_{14}O_{12}P_2$ [R.N. 126722-35-8]: Crystals, mp 174-176 °C,[1287] $[\alpha]_D^{25}$ +3.4° ($H_2O$).[1274] Spectra: IR,[1287] MS (FAB).[1275] Chromatography: PC.[1274]

D-*myo*-Inositol 3,4-Bisphosphate

$Ins(3,4)P_2$ [R.N. 69256-53-7]: HPLC.[1250] Additional data for DL-$Ins(3,4)P_2$: $^1H$ and $^{31}P$ NMR,[1285] IEC.[1227]

$(C_6H_{11}NH_2)_4C_6H_{14}O_{12}P_2$: Crystals, mp 158-161 °C, $[\alpha]_D^{20}$ +3.9° ($H_2O$), IR, PC.[1287]

D-*myo*-Inositol 4,5-Bisphosphate

$Ins(4,5)P_2$ [R.N. 69256-54-8]: Conformation.[1288] Chromatography: HPLC,[161] GC.[1269] Additional data for DL-$Ins(4,5)P_2$ [R.N. 109584-32-9]: p$K_a$ 8.01, 8.15 (potentiometric).[1286] Spectra: $^1H$ NMR,[1285] 2d-$^1H$ NMR (fig.),[687] $^{13}C$ NMR,[1195] $^{31}P$ NMR.[1286] Chromatography: IEC.[1227]

$(NH_3)_4C_6H_{14}O_{12}P_2$: Spectra: FAB-MS/MS (fig.).[1260]

$(C_6H_{11}NH_2)_4C_6H_{14}O_{12}P_2$: Crystals, mp 138-140 °C,[1287] $[\alpha]_D^{25}$ −15.2° ($H_2O$).[1274] Spectra: IR.[1287] Chromatography: PC.[1274]

## Synthesis

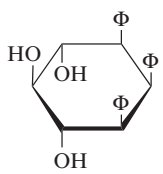
$Ins(1,4)P_2$ may be prepared by phosphorylation of D-2,3:5,6-di-*O*-cyclohexylidene-*myo*-inositol with diphenyl phosphorochloridate[1287] or of D-2,3-*O*-camphanylidene-5,6-*O*-isopropylidene-*myo*-inositol with 2-dimethylamino-5,6-benzo-1,3,2-dioxaphosphepane.[1259] $Ins(3,4)P_2$ may be prepared (a) by phosphorylation of D-1,2:5,6-di-*O*-cyclohexylidene-*myo*-inositol with diphenyl phosphorochloridate[1287] or (b) by partial dephosphorylation of D-$Ins(1,3,4)P_3$ with alkaline phosphatase.[1250] $Ins(4,5)P_2$ may be prepared by phosphorylation of D-1,6:2,3-di-*O*-cyclohexylidene-*myo*-inositol with diphenyl phosphorochloridate in pyridine.[1287] No synthesis of $Ins(1,2)P_2$ has been published.

## Conformation

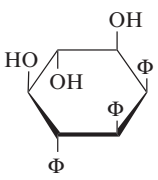
Ins(1,2)P adopts the $1_{ax}/5_{eq}$ conformation over the entire pH range 1.0-13.0, according to $^1H$ NMR analysis. There is no evidence for the $5_{ax}/1_{eq}$ form.[1281]

# *myo*-Inositol Trisphosphates

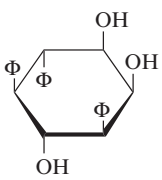
There are 20 *myo*-inositol trisphosphates, of which 5 are important plant metabolites (Φ = OP(O)(OH)$_2$):



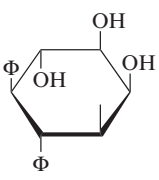

**Ins(1,2,3)$P_3$**
(*meso*)



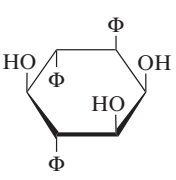

**D-Ins(1,2,6)$P_3$**
L-Ins(2,3,4)$P_3$




**D-Ins(1,4,5)$P_3$**
L-Ins(3,5,6)$P_3$




**D-Ins(1,5,6)$P_3$**
L-Ins(3,4,5)$P_3$




**D-Ins(3,4,6)$P_3$**
L-Ins(1,4,6)$P_3$

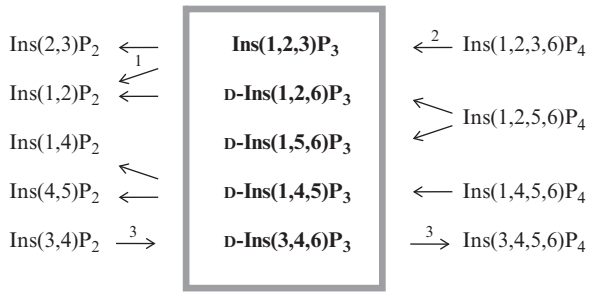



**FIGURE 3-3** ***myo*-Inositol Trisphosphates**. (1) 6-Phytase [E.C. 3.1.3.26]. (2) 5-Phytase.[1291] (3) Phytic acid synthase.[1238]

*myo*-Inositol 1,2,3-trisphosphate (Ins(1,2,3)$P_3$), $C_6H_{15}O_{15}P_3$; unlisted in Beilstein. *myo-Inositol 1,2,3-Tris(Dihydrogen Phosphate)* [1962].

D-*myo*-Inositol 1,2,6-Trisphosphate (Ins(1,2,6)$P_3$), $C_6H_{15}O_{15}P_3$; unlisted in Beilstein. D-*myo-Inositol 1,2,6-Tris(Dihydrogen Phosphate)* [1962].

D-*myo*-Inositol 1,4,5-Trisphosphate (Ins(1,4,5)$P_3$), $C_6H_{15}O_{15}P_3$; unlisted in Beilstein. D-*myo-Inositol 1,4,5-Tris(Dihydrogen Phosphate)* [1961].

D-*myo*-Inositol 1,5,6-Trisphosphate (Ins(1,5,6)$P_3$), $C_6H_{15}O_{15}P_3$; unlisted in Beilstein. D-*myo-Inositol 1,5,6-Tris(Dihydrogen Phosphate)* [1988].

D-*myo*-Inositol 3,4,6-Trisphosphate (Ins(3,4,6)$P_3$), $C_6H_{15}O_{15}P_3$; unlisted in Beilstein. D-*myo-Inositol 3,4,6-Tris(Dihydrogen Phosphate)* [1996].

## Occurrence

Ins(1,2,3)$P_3$ and Ins(1,2,6)$P_3$ have been identified in barley aleurone tissue[1208] and Ins(1,3,4)$P_3$ in pea flour.[1289] Ins(1,4,5)$P_3$ occurs in cauliflower hypocotyl,[1244] in pea flour,[1289] in apple buds,[1240] in carnation flower petals,[1290] in rain tree pulvini,[1219] and in Madagascar periwinkle,[1200] tobacco,[1200] and lucerne[1239] cell suspension cultures. Ins(2,4,5)$P_3$ has been identified in pea flour[1289] and Ins(3,4,6)$P_3$ in giant duckweed (Fig. 3-3).[1243]

## Physical Properties

### *myo*-Inositol 1,2,3-Trisphosphate

Ins(1,2,3)$P_3$ [R.N. 41613-02-9]: $[\alpha]_D^{25}$ 0° ($H_2O$).[1284] Spectra: $^1$H NMR (fig.),[1292] 2d-$^1$H NMR (fig.),[1292] $^{13}$C NMR (calc.).[1195] Chromatography: IEC,[1227] HPLC.[161] Electrophoresis: PE.[1284]

$Ba_3C_6H_9O_{15}P_3$: Slightly soluble in $H_2O$.[676]

$(NH_4)_6C_6H_9O_{15}P_3$: $[\alpha]_D^{25}$ 0° ($H_2O$).[1284]

$(C_6H_{11}NH_3)_6C_6H_9O_{15}P_3$: Crystals. Spectra: $^1$H NMR, $^{31}$P NMR.[1293]

### D-*myo*-Inositol 1,2,6-Trisphosphate

Ins(1,2,6)$P_3$ [R.N. 28841-62-5]: $[\alpha]_D^{22}$ −3.2° ($H_2O$)[1294]; p$K_a$ 5.28, 6.54, and 8.44 (potentiometric, 37 °C); microscopic protonation constants given for the 12

dissociation equilibria.[1295] Spectra: $^{1}$H NMR (fig.),[1292] 2d-$^{1}$H NMR (fig.),[1292] $^{13}$C NMR.[1195] Chromatography: HPLC,[161] LC/MS.[1251] Electrophoresis: PE.[1291] Additional data for DL-Ins(1,2,6)$P_3$ [R.N. 121321-74-9]: $^{31}$P NMR (fig.),[1252] IEC,[1227] CZE/MS.[1270]

D-*myo*-Inositol 1,4,5-Trisphosphate

Ins(1,4,5)$P_3$ [R.N. 85166-31-0]: Spectra: $^{1}$H NMR (fig.),[1296] $^{13}$C NMR (fig.),[1296] $^{31}$P NMR (fig.),[1296] MS (FAB, fig.).[690] Chromatography: PC,[1274] IEC,[1248] TLC,[1297] HPTLC,[407] HPLC,[1250] IC,[107] GC/MS,[690] SFC/MS.[1298] Electrophoresis: PE.[1239] Additional data for DL-Ins(1,4,5)$P_3$ [R.N. 109583-09-7]: Potentiometric titration,[1286] high-pH IEC,[730] CE,[1254] CZE.[1299]

$Ba_3C_6H_9O_{15}P_3$: Slightly soluble in $H_2O$.[676]

$(NH_4)_6C_6H_9O_{15}P_3$: $[\alpha]_D^{25}$ −9.4° ($H_2O$).[1297] Spectra: FAB-MS/MS (fig.).[1260]

$(C_6H_{11}NH_3)_6C_6H_9O_{15}P_3$ [R.N. 120710-76-1]: $[\alpha]_D^{25}$ −27.4° ($H_2O$).[1274] PC.[1274]

D-*myo*-Inositol 1,5,6-Trisphosphate

Ins(1,5,6)$P_3$ [R.N. 121251-13-6]: Spectra: $^{1}$H NMR (fig.),[1292] 2d-$^{1}$H NMR (fig.),[1292] $^{13}$C NMR and $^{31}$P NMR.[1300] Chromatography: HPLC.[161] Additional data for DL-Ins(1,5,6)$P_3$ [R.N. 118354-68-0]: $^{1}$H NMR,[687,1229] IEC,[1227] high-pH IEC,[730] IC.[1229]

$Na_6C_6H_9O_{15}P_3$: $[\alpha]_D$ −2.8° ($H_2O$).[1300]

D-*myo*-Inositol 3,4,6-Trisphosphate

Ins(3,4,6)$P_3$ [R.N. 114418-84-7]: Chromatography: IEC,[1301] HPLC.[1243] Additional data for DL-Ins(3,4,6)$P_3$ [R.N. 131321-75-0]: $^{1}$H NMR,[687] IEC.[1227]

$Na_3C_6H_{12}O_{15}P_3$: $[\alpha]_D^{20}$ +9.4° ($H_2O$).[1302] Additional data for DL-$Na_3C_6H_{12}O_{15}P_3$: Fine crystals, mp > 240 °C, Spectra: $^{1}$H, $^{13}$C, and $^{31}$P NMR.[1302]

$(Et_3N)_xC_6H_9O_{15}P_3$: $[\alpha]_D$ +25.0° (TEAB).[1301] Spectra: $^{1}$H NMR, $^{31}$P NMR, MS (FAB).[1301]

## Synthesis

Ins(1,2,3)$P_3$ may be prepared by phosphorylation of 4,5,6-tri-*O*-benzoyl-*myo*-inositol with dibenzyl *N,N*-diisopropylphosphoramidite.[1293] Ins(1,4,5)$P_3$ may be prepared (a) by phosphorylation of D-2,3,6-tri-*O*-benzyl-*myo*-inositol or other fully protected *myo*-inositol with *N,N′*-diphenylphosphorodiamidic chloride,[1303] tetrabenzyl pyrophosphate,[1275,1303] dibenzyl *N,N*-diisopropylphosphoramidite,[1304] dibenzyl *N,N*-diethylphosphoramidite,[1305] *O*-xylylene *N,N*-diethylphosphoramidite,[1297,1303] or bis(2-cyanoethyl) *N,N*-diethylphosphoramidite[1306] or (b) by selective phosphorylation of a partially protected *myo*-inositol with *N,N′*-diphenylphosphorodiamidic chloride.[1307] Ins(1,5,6)$P_3$ may be prepared by phosphorylation of D-2,3-*O*-camphanylidene-4-(*t*-butyldimethylsilyl)-*myo*-inositol with 2-dimethylamino-5.6-benzo-1,3,2-dioxaphosphepane.[1293] Ins(3,4,6)$P_3$ may be prepared (a) by phosphorylation of 1D-5-*O*-acetyl-1,2-*O*-cyclohexylidene-*myo*-inositol with *O*-xylylene *N,N*-diethylphosphoramidite in the presence of 1*H*-tetrazole[1302] or (b) of D-1,2,5-tri-*O*-benzyl-*myo*-inositol with di-*O*-benzyl *N,N*-diisopropylphosphoramidite in the presence of 1*H*-tetrazole.[1301]

### Conformation

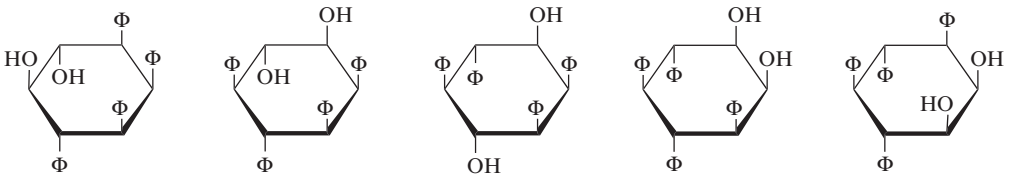
The 1,2,3-, 1,2,6-, and 1,4,5-*myo*-inositol trisphosphates all adopt the $1_{ax}/5_{eq}$ conformation over the entire pH range from 1.0 to 13.0, with no evidence for the $5_{ax}/1_{eq}$ conformer.[1281]

### Ins(2,4,5)$P_3$

Maitra *et al.*[1308] isolated an $InsP_3$ from the products of hydrolysis of phytic acid by mung bean phytase tentatively identified as Ins(2,4,5)$P_3$, implying the existence of an alternative pathway for phytate metabolism. The status of this finding remains unresolved.

## *myo*-Inositol Tetrakisphosphates

There are 15 *myo*-inositol tetrakisphosphates, of which 5 are important plant metabolites ($\Phi = OP(O)(OH)_2$) (Fig. 3-4):




**D-Ins(1,2,3,6)$P_4$** L-Ins(1,2,3,4)$P_4$ | **D-Ins(1,2,5,6)$P_4$** L-Ins(2,3,4,5)$P_4$ | **D-Ins(1,3,4,5)$P_4$** L-Ins(1,3,5,6)$P_4$ | **D-Ins(1,4,5,6)$P_4$** L-Ins(3,4,5.6)$P_4$ | **D-Ins(3,4,5,6)$P_4$** L-Ins(1,4,5,6)$P_4$

D-*myo*-Inositol 1,2,3,6-tetrakisphosphate (Ins(1,2,3,6)$P_4$), $C_6H_{16}O_{18}P_4$; not listed in Beilstein. D-*myo-Inositol 1,2,3,6-Tetrakis(Dihydrogen Phosphate)* [1969].

D-*myo*-Inositol 1,2,5,6-Tetrakisphosphate (Ins(1,2,5,6)$P_4$), $C_6H_{16}O_{18}P_4$; not listed in Beilstein. D-*myo-Inositol 1,2,5,6-Tetrakis(Dihydrogen Phosphate)* [1962].

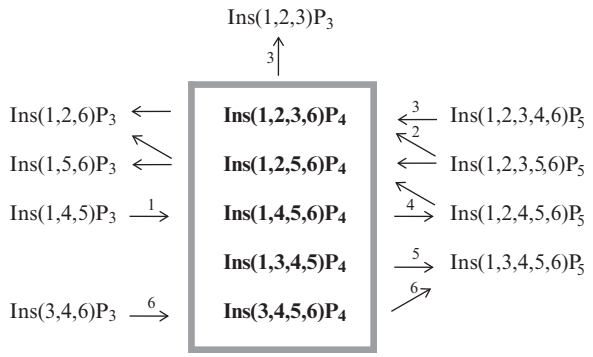



**FIGURE 3-4** ***myo*-Inositol Tetrakisphosphates.** (1) Ins(1,4,5)$P_3$ 6-kinase, ATP, Mg(II). (2) 6-Phytase [E.C. 3.1.3.26]. (3) 5-Phytase.[1291] (4) Ins(1,3,4,5,6)$P_5$ 6-kinase, ATP, Mg(II).[1309] (5) Ins(1,3,4,5)$P_4$ 6-kinase.[1310] (6) Phytic acid synthase.[1238]

D-*myo*-Inositol 1,3,4,5-Tetrakisphosphate (Ins(1,3,4,5)$P_4$), $C_6H_{16}O_{18}P_4$; not listed in Beilstein. D-*myo-Inositol 1,3,4,5-Tetrakis(Dihydrogen Phosphate)* [1988].

D-*myo*-Inositol 1,4,5,6-Tetrakisphosphate (Ins(1,4,5,6)$P_4$), $C_6H_{16}O_{18}P_4$; not listed in Beilstein. D-*myo-Inositol 1,4,5,6-Tetrakis(Dihydrogen Phosphate)* [1988].

D-*myo*-Inositol 3,4,5,6-Tetrakisphosphate (Ins(3,4,5,6)$P_4$), $C_6H_{16}O_{18}P_4$; not listed in Beilstein. D-*myo-Inositol 3,4,5,6-Tetrakis(Dihydrogen Phosphate)* [1996].

## Occurrence

Ins(1,2,3,6)$P_4$ and Ins(1,2,5,6)$P_4$ were identified in barley aleurone tissue,[1208] Ins(1,2,5,6)$P_4$ in pea flour,[1289] and Ins(3,4,5,6)$P_4$ in giant duckweed.[1243]

## Physical Properties

### D-*myo*-Inositol 1,2,3,6-Tetrakisphosphate

Ins(1,2,3,6)$P_4$ [R.N. 41613-03-0]: $[\alpha]_D^{25}$ +6.0° ($H_2O$).[1284] Spectra: 2d-$^1$H NMR (fig.).[1292] Chromatography: IEC.[719] Electrophoresis: PE.[1284] Additional data for DL-Ins(1,2,3,6)$P_4$ [R.N. 118354-66-8]: $^1$H NMR,[1229] IC.[1229]

Ba salt: Amorphous solid, insol. in aqueous ethanol.[676]

$(NH_4)_8C_6H_{12}O_{18}P_4$: $[\alpha]_D^{25}$ −11.3° ($H_2O$).[1284]

### D-*myo*-Inositol 1,2,5,6-Tetrakisphosphate

Ins(1,2,5,6)$P_4$ [R.N. 28841-60-3]: $[\alpha]_D^{25}$ −3.5° ($H_2O$),[719] $[M]_{300}^{25}$ −233° ($H_2O$).[1311] Spectra: ORD,[1311] 2d-$^1$H NMR (fig.),[1292] FAB-MS.[690] Chromatography: IEC,[719] HPLC.[161] Electrophoresis: PE.[1291] Additional data for DL-Ins(1,2,5,6)$P_4$ [R.N. 118354-64-6]: p$K_a$ (potentiometric, 37 °C) 5.23, 6.06, 7.65, and 9.39,[1312] $^1$H NMR,[687,1229] $^{13}$C NMR,[1195] IC,[1229] high-pH IEC,[730] CZE/MS.[1270]

Ba salt: Amorphous solid, insol. in aqueous ethanol.[676]

$(C_6H_{11}NH_3)_8C_6H_{12}O_{18}P_4$: $[\alpha]_D^{25}$ −14.8° ($H_2O$); may contain some 1,2,3,5 or 1,2,3,6 isomer.[723]

### D-*myo*-Inositol 1,3,4,5-Tetrakisphosphate

Ins(1,3,4,5)$P_4$ [R.N. 99610-76-1]: p$K_a$ (potentiometric, 37 °C): 5.23, 6.36, 7.66, 9.92.[1312] Spectra: $^1$H (fig.), $^{13}$C (fig.), $^{31}$P (fig.), and 2d-$^1$H NMR (fig.).[1313] Chromatography: IEC,[1267] HPLC.[161] Additional data for DL-Ins(1,3,4,5)$P_4$ [R.N. 115184-69-5]: 2d-$^1$H NMR (fig.),[1228] IC.[1229]

$K_4C_6H_{12}O_{18}P_4$: $[\alpha]_D^{20}$ −3.85° ($H_2O$).[1314] Spectra: IR, $^1$H, $^{13}$C, and $^{31}$P NMR, ES-MS.[1314]

$(NH_3)_8C_6H_{18}O_{18}P_4$: $[\alpha]_D^{24}$ −13° ($H_2O$).[1315]

$(C_6H_{11}NH_2)_{4.5}C_6H_{18}O_{18}P_4$: mp 173.7-175.7 °C, $[\alpha]_D^{25}$ −2.5° ($H_2O$).[1316] Spectra: $^1$H, $^{13}$C, and $^{31}$P NMR, FAB-MS.[1316]

D-*myo*-Inositol 1,4,5,6-Tetrakisphosphate
Ins(1,4,5,6)$P_4$ [R.N. 109837-24-3]: Spectra: $^1H$, $^{13}C$, $^{31}P$ NMR (figs.).[1317] Chromatography: IEC, [1317] HPLC.[161] Additional data for DL-Ins(1,4,5,6)$P_4$ [R.N. 113666-11-8]: IC,[1229] high-pH IEC.[730]

D-*myo*-Inositol 3,4,5,6-Tetrakisphosphate
Ins(3,4,5,6)$P_4$: Spectra: $^1H$ and $^{31}P$ NMR.[1259] Chromatography: HPTLC,[407] HPLC.[1243]
$Na_8C_6H_{18}O_{18}P_4$: Solid, mp > 270 °C, $[\alpha]_D^{24}$ +9.8° ($H_2O$).[1318]

## Synthesis

Ins(1,2,5,6)$P_4$ is formed together with some Ins(1,2,3,6)$P_4$ by partial dephosphorylation of phytic acid with phytase.[723,1284] Ins(1,4,5,6)$P_4$ and Ins(3,4,5,6)$P_4$ may be prepared by phosphorylation of D-2,3- and D-1,2-*O*-cyclohexylidene-*myo*-inositol, respectively, with dibenzyl *N*,*N*-diisopropylphosphoramidite in the presence of 1*H*-tetrazole.[1318] Ins(1,3,4,5)$P_4$ may be prepared (a) by phosphorylation of D(−)-2,6-di-*O*-benzyl-*myo*-inositol with dibenzyl *N*,*N*′-diisopropylphosphoramidite,[1319] 2-diethylamino-1,3,2-benzodioxaphosphepane,[1314] or tetrabenzyl pyrophosphate[1315] or (b) by enzymic phosphorylation of D-Ins(1,4,5)$P_3$ with Ins(1,4,5)$P_3$ kinase.[1264] No synthesis of Ins(1,2,3,6)$P_4$ has been published.

## Conformation

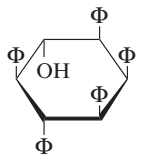
Both Ins(1,2,3,6)$P_4$ and Ins(1,2,5,6)$P_4$ adopt the $1_{ax}/5_{eq}$ conformation over the entire pH range from 1.0 to 13.0, with no evidence for the $5_{ax}/1_{eq}$conformer.[1281]

## Phosphorylation

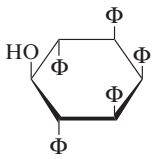
DL-Ins(1,4,5,6)$P_4$ is phosphorylated by Ins(1,3,4,5,6)$P_5$ 2-kinase from immature soybeans giving a pentakisphosphate identified by IEC as DL-Ins(1,2,4,5,6)$P_5$.[1309]

# *myo*-Inositol Pentakisphosphates

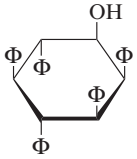
There are six *myo*-inositol pentakisphosphates, of which four are important plant metabolites (Φ = OP(O)$(OH)_2$):



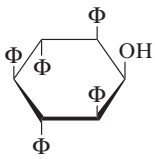

**L-Ins(1,2,3,4,5)$P_5$**
D-Ins(1,2,3,5,6)$P_4$




**Ins(1,2,3,4,6)$P_5$**
(*meso*)




**D-Ins(1,2,4,5,6)$P_5$**
L-Ins(2,3,4,5,6)$P_5$




**Ins(1,3,4,5,6)$P_5$**
(*meso*)

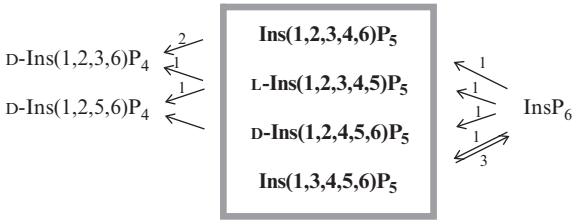



**FIGURE 3-5** ***myo*-Inositol Pentakisphosphates**. (1) 6-Phytase [E.C. 3.1.3.26]. (2) 5-Phytase.[1291] (3) 2-Kinase, ATP, Mg(II).[1309]

L-*myo*-Inositol 1,2,3,4,5-Pentakisphosphate (Ins(1,2,3,4,5)$P_5$), $C_6H_{17}O_{21}P_5$; not listed in Beilstein. L-*myo-Inositol 1,2,3,4,5-Pentakis(Dihydrogen Phosphate)* [1962].

*myo*-Inositol 1,2,3,4,6-Pentakisphosphate (Ins(1,2,3,4,6)$P_5$), $C_6H_{17}O_{21}P_5$; not listed in Beilstein. *myo-Inositol 1,2,3,4,6-Pentakis(Dihydrogen Phosphate)* [1968].

D-*myo*-Inositol 1,2,4,5,6-Pentakisphosphate (Ins(1,2,4,5,6)$P_5$), $C_6H_{17}O_{21}P_5$; not listed in Beilstein. D-*myo-Inositol 1,2,4,5,6-Pentakis(Dihydrogen Phosphate)* [1968].

*myo*-Inositol 1,3,4,5,6-Pentakisphosphate (Ins(1,3,4,5,6)$P_5$), $C_6H_{17}O_{21}P_5$; not listed in Beilstein. *myo-Inositol 1,3,4,5,6-Pentakis(Dihydrogen Phosphate)*.

## Occurrence

Ins(1,2,3,4,6)$P_5$ (one of the *meso* compounds) was identified in barley aleurone tissue[1208] and in soybean seed,[1229] and Ins(1,3,4,5,6)$P_5$ (the other *meso* compound) was identified in barley aleurone tissue,[1208] in soybean seed[1229] and in giant duckweed.[1243] D- and/or L-Ins(1,2,3,4,5)$P_5$ was identified in barley aleurone tissue,[1208] in soybean seed,[1229] and in mung bean sprout.[1320] D- and/or L-Ins(1,2,4,5,6)$P_5$ was identified in soybean seed,[1229] in mung bean sprout,[1320] and in giant duckweed (Fig. 3-5).[1243]

## Physical Properties

### L-*myo*-Inositol 1,2,3,4,5-Pentakisphosphate

Ins(1,2,3,5,6)$P_5$ [R.N. 26326-85-2]: Solid,[1321] $[\alpha]_D^{25}$ +1.6° ($H_2O$).[1284] Spectra: $^1$H NMR, $^{31}$P NMR,[1321] FAB-MS (fig.).[690] Chromatography: IEC,[718] HPLC,[1320] IC.[1229] Electrophoresis: PE.[720] Additional data on DL-(1,2,3,5,6)Ins$P_5$ [R.N. 23486-93-3]: $^{13}$C NMR.[1195]

$Na_8C_6H_9O_{21}P_5$: White powder, FAB-MS.[1210]

Ba salt: Amorphous solid, insol. in $H_2O$.[676]

$(NH_4)_{10}C_6H_{12}O_{21}P_5$: $[\alpha]_D^{25}$ +3.7° ($H_2O$).[1284]

### *myo*-Inositol 1,2,3,4,6-Pentakisphosphate

Ins(1,2,3,4,6)$P_5$ [R.N. 20298-97-9]: $[\alpha]_D^{25}$ 0° ($H_2O$).[1284] Spectra: $^1$H NMR,[1229] 2d-$^1$H NMR (fig.),[1291] $^{13}$C NMR,[1195] $^{31}$P NMR,[1291] FAB-MS.[690] Chromatography: IEC,[719] HPLC,[1320] IC.[1229] Electrophoresis: PE.[720]

Ba salt: Amorphous solid, insol. in $H_2O$.[676]

$(NH_4)_{10}C_6H_{12}O_{21}P_5$: $[\alpha]_D^{25}$ 0° ($H_2O$).[1284]

D-*myo*-Inositol 1,2,4,5,6-Pentakisphosphate

Ins(1,2,4,5,6)$P_5$ [R.N. 26326-86-3]: $[\alpha]_D$ −7.4° ($H_2O$),[1322] $[M]^{25}_{300}$ −115° to −160° ($H_2O$).[1311] Spectra: $^1$H NMR,[1320] 2d-$^1$H NMR (fig.),[1320] $^{31}$P NMR (fig.),[1320] FAB-MS,[690] ORD.[1311] Chromatography: IEC,[1323] HPLC.[1320] Additional data for DL-Ins(1,2,4,5,6)$P_5$ [R.N. 23393-17-1]: $^{13}$C NMR,[1195] IC,[1229] PE.[720]

Ba salt: Amorphous solid, insol. in $H_2O$.[676]

$(NH_4)_{10}C_6H_{12}O_{21}P_5$: $[\alpha]_D$ −4.0° ($H_2O$).[1322]

*myo*-Inositol 1,3,4,5,6-Pentakisphosphate

Ins(1,3,4,5,6)$P_5$ [R.N. 20298-95-7]: $[M]^{25}_D$ 0°.[1284] Spectra: $^1$H NMR (fig.),[1317] $^{13}$C NMR (fig.),[1317] $^{31}$P NMR (fig.),[679] FAB-MS.[690] Chromatography: PC,[679] TLC,[1324] IEC,[1323] high-pH IEC,[730] HPTLC,[407] HPLC,[1320] IC,[1229] GFC.[1225] Electrophoresis: PE.[720]

Ba salt: Amorphous solid, insol. $H_2O$.[676] Spectra: IR.[679]

$Na_{10}C_6H_7O_{21}P_5$ [23103-36-8]: Amorphous hygroscopic solid, $[\alpha]^{20}_D$ 0.0° ($H_2O$).[679] Spectra: IR (Table 3-4).[679]

## Synthesis

Ins(1,2,3,4,5)$P_5$ may be prepared by enzymatic hydrolysis of phytic acid with wheat bran phytase [E.C. 3.1.3.26] or wheat germ phosphatase [E.C. 3.1.3.2].[1210] DL-Ins(1,2,3,4,5)$P_5$ and DL-Ins(1,2,4,5,6)$P_5$ have been prepared by the reaction of *N*-benzoylphosphoramidic acid with DL-4-*O*-benzyl-*myo*-inositol and DL-3-*O*-benzyl-*myo*-inositol, respectively, in DMF.[716]

No synthesis has yet been published for either of the other two pentakisphosphates.

## Phosphorylation

All four pentakisphosphates are phosphorylated by mung bean kinase/Mg(II) to phytic acid.[1320,1337] The relative first-order rate constants for DL-Ins(1,2,4,5,6)$P_5$, DL-Ins (1,2,3,4,5)$P_5$, Ins(1,2,3,4,6)$P_5$, and Ins(1,3,4,5,6)$P_5$ are 1:11:12:33, respectively.[1320]

## Analytical Methods

The four Ins$P_5$'s can be separated from each other by HPLC on a Mono Q anion exchange column upon gradient elution with 0.0002→0.4*M* HCl[161] or by IC on a Dionex AS-3 column on gradient elution with 0→0.155*N* $HNO_3$.[1229] The order of elution in both cases is Ins(1,2,3,4,6)$P_5$ > Ins(1,2,3,4,5)$P_5$ > Ins(1,2,4,5,6)$P_5$ > Ins (1,3,4,5,6)$P_5$. They can also be separated on a Partisphere HPLC column upon gradient elution with 0-0.5*M* ammonium phosphate, pH 3.2, but require sequential runs on a weak (WAX) and a strong (SAX) anion exchanger (in any order) for complete separation.[1320]

**Table 3-4** Lower *myo*-Inositol Phosphates in Plants*

| No. | Plant part | Method | $InsP_1$ | $InsP_2$ | $InsP_3$ | $InsP_4$ | $InsP_5$ | $InsP_6$ | References |
|---|---|---|---|---|---|---|---|---|---|
| *Agropyron desertorum* (Fisch.) Schult. (Crested Wheatgrass) | | | | | | | | | |
| 1 | Seed[a] | IEC | | 0.10 | 0.21 | 0.47 | | | 831 |
| *Brassica napus* L. (Rape) | | | | | | | | | |
| 8 | Whole seed[b] | HPLC | | | 0 | 0 | 0.63-0.86 | 24.2-34.5 | 1325 |
| 8 | –, dehulled[b] | HPLC | | | 0 | 0 | 0.94-1.24 | 30.5-38.9 | 1325 |
| 8 | –, hull[b] | HPLC | | | 0 | 0 | 0.08-0.45 | 2.4-10.1 | 1325 |
| *Brassica napus* L. ssp. *oleifera* (Winter Rape) | | | | | | | | | |
| 1 | Leaf | IEC | ++ | + | + | | | | 1326 |
| *Brassica oleracea* L. ssp. *botrytis* Cauliflower | | | | | | | | | |
| 1 | Hypocotyl | $^{32}P_i$ | + | + | + | | | | 1244 |
| *Cajanus cajan* (L.) Mill. (Pigeon Pea) | | | | | | | | | |
| 1 | Seed | HPLC | | | 0 | 0.04 | 2.41 | 7.96 | 1327 |
| *Catharanthus roseus* (L.) G. Don (Madagascar Periwinkle) | | | | | | | | | |
| 1 | Cell suspension culture | IEC | 12.8 | 0.29 | 0.16 | | | | 1200 |
| *Ceratophyllum* spp. (Hornwort) | | | | | | | | | |
| 1 | Whole plant[a] | IEC | | | 0.028 | | + | | 912 |
| *Chenopodium quinoa* Willd. (Quinoa) | | | | | | | | | |
| 1 | Seed, sweet | HPLC | | | 0 | 0.002 | 0.002 | 0.206 | 916 |
| 1 | Seed, bitter | HPLC | | | 0 | 0.002 | 0.004 | 0.160 | 916 |
| *Cicer arietinum* L. (Chickpea) | | | | | | | | | |
| 1 | Seed | HPLC | | | 0 | 0.04 | 1.76 | 6.00 | 1327 |
| 2 | Seed[c] | HPLC | | | 0.025-0.027 | 0-0.011 | 0.031-0.068 | 0.379-0.389 | 922 |
| *Cocos nucifera* L. (Coconut) | | | | | | | | | |
| 1 | Copra cake | HPLC | | | 1.76 | 0.91 | 1.65 | 9.71 | 1328 |
| *Coffea arabica* L. (Coffee) | | | | | | | | | |
| 3 | Bean[c] | HPLC | | | 0 | 0 | 0.025-0.039 | 0.255-0.292 | 935 |
| *Coffea robusta* (Coffee) | | | | | | | | | |
| 2 | Bean[c] | HPLC | | | 0 | 0-0.040 | 0.031-0.110 | 0.306-0.368 | 935 |
| *Corylus avellana* L. (Hazel) | | | | | | | | | |
| 1 | Shelled nut[a] | HPLC | | | 0 | 0 | 0 | 2.58 | 938 |
| *Daucus carota* L. (Carrot) | | | | | | | | | |
| 1 | Cell suspension culture | $^3$H-Ins | + | | | | | | 950 |
| *Dianthus caryophyllus* L. (Carnation) | | | | | | | | | |
| 1 | Flower petal | $^3$H-Ins | | | + | | | | 1290 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Glycine max* (L.) Merr. (Soybean) | | | | | | | | | |
| 1 | Seed | IC | | | + | + | + | + | 1229 |
| 1 | Seed, immature[d] | IEC | 1.9 | Trace | 0 | Trace | 4.9 | | 1329 |
| 4 | Seed meal | HPLC | | | 0 | 0-0.60 | 1.09-3.98 | 11.78-16.84 | 1328 |
| *Gossypium hirsutum* L. (Upland Cotton) | | | | | | | | | |
| 1 | Glandless seed, defatted | IEC, PE | | 0 | 0 | + | + | | 1330 |
| *Helianthus annuus* L. (Sunflower) | | | | | | | | | |
| 1 | Seed meal | HPLC | | | 0.20 | 0.48 | 5.63 | 40.43 | 1328 |
| *Hordeum vulgare* L. (Barley) | | | | | | | | | |
| 4 | Grain | HPLC | | | 0 | 0 | 0 | 3.78-5.73 | 1328 |
| 1 | Grain[c] | HPLC | | | 0 | 0 | 0.087 | 0.887 | 1331 |
| 1 | Unripe caryopsis | HPLC | | | | | + | | 857 |
| 1 | Aleurone tissue | HPLC | + | + | + | + | + | + | 1208 |
| 1 | Mesophyll cells | $^{3}$H-Ins | | + | | | | | 1283 |
| *Lemna minor* L. (Lesser Duckweed) | | | | | | | | | |
| 1 | Whole plant | IEC, GFC | + | + | + | + | + | | 683 |
| *Lemna* spp. (Duckweed) | | | | | | | | | |
| 1 | Whole plant [a] | IEC | | | 0.119 | | + | | 912 |
| *Lens culinaris* Medic. (Lentil) | | | | | | | | | |
| 1 | Seed | HPLC | | | 0.32 | 0.21 | 1.39 | 8.37 | 1327 |
| 1 | Seed[c] | HPLC | | | 0.016 | 0.019 | 0.048 | 0.244 | 922 |
| 1 | Raw flour[a] | HPLC | | | 0.37 | 0.50 | 1.07 | 10.77 | 1332 |
| *Lilium longiflorum* Thunb. (Trumpet Lily) | | | | | | | | | |
| 1 | Pollen | $^{3}$H-Ins | + | | | | | | 1217 |
| *Lupinus albus* L. (White Lupine) | | | | | | | | | |
| 1 | Seed[c] | HPLC | | | 0 | 0 | 0 | 0.314 | 922 |
| *Lupinus luteus* L. (Yellow Lupine) | | | | | | | | | |
| 1 | Seed [a] | HPLC | | | | | 0.09 | 21.72 | 1333 |
| 1 | Seed [c] | HPLC | | | 0 | 0 | 0.06 | 0.717 | 922 |
| *Malus domestica* Borkh. (Apple) | | | | | | | | | |
| 1 | Bud, dormant | HPLC | 0.72 | 0.00035 | 0.0033 | | | | 1240 |
| *Medicago sativa* L. (Alfalfa) | | | | | | | | | |
| 1 | Seed meal | HPLC | | | 0 | 0.26 | 0 | 0.80 | 1328 |
| 1 | Cell suspension culture | $^{3}$H-Ins | | + | + | | | | 1239 |

*nmol/g fresh weight basis unless stated otherwise; [a]μmol/g; [b]mg/g; [c]Percentage of plant tissue; [d]Percentage of total P.

*Continued*

**Table 3-4** Lower *myo*-Inositol Phosphates in Plants*—cont'd

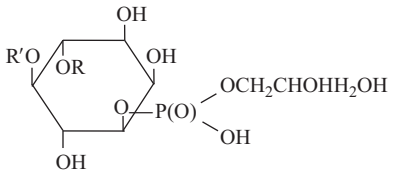
| No. | Plant part | Method | $InsP_1$ | $InsP_2$ | $InsP_3$ | $InsP_4$ | $InsP_5$ | $InsP_6$ | References |
|---|---|---|---|---|---|---|---|---|---|
| *Myriophyllum* spp. (Water Milfoil) | | | | | | | | | |
| 1 | Whole plant[a] | IEC | | | 0.071 | | + | | 912 |
| *Nicotiana tabacum* L. (Tobacco) | | | | | | | | | |
| 1 | Cell suspension culture | $^3$H-Ins | + | + | + | | | | 1200 |
| *Oryza sativa* L. (Rice) | | | | | | | | | |
| 1 | Seed | IEC | 0 | 0 | 0 | 0 | 0 | | 1218 |
| 1 | Brown seed, nonwaxy | IEC | | | | + | + | | 1046 |
| 1 | –, embryo[d] | IEC | | | | 0.019 | 0.020 | | 1046 |
| 1 | –, endosperm | IEC | | | | 0 | 0 | | 1046 |
| 1 | –, bran | IEC | | | | + | + | | 1046 |
| 3 | Seed, milled | HPLC | | | 0-0.93 | 0-0.49 | 1.23-3.08 | 13.83-28.00 | 1328 |
| 1 | Bran | HPLC | | | 0 | 0.65 | 7.75 | 59.99 | 1328 |
| 1 | Ripening grain | $^3$H-Ins | + | | | | | | 1242 |
| 1 | Cell suspension culture | $^3$H-Ins | + | | | | | | 1186 |
| *Phaseolus lunatus* L. (Lima Bean) | | | | | | | | | |
| 1 | Bean | HPLC | | | 0 | 0.23 | 2.13 | 9.96 | 1327 |
| *Phaseolus vulgaris* L. (Beans (Common)) | | | | | | | | | |
| 6 | Bean | HPLC | | | 0 | 0.02-0.19 | 1.80-2.19 | 11.7-14.2 | 1327 |
| 2 | Bean[c] | HPLC | | | 0.009 | 0 | 0.019-0.020 | 0.564-0.628 | 922 |
| 1 | Root[a] | IEC | | 3.70 | 3.80 | 0.74 | | | 1334 |
| *Pisum sativum* L. (Peas) | | | | | | | | | |
| 1 | Soaked flour | HPLC | | + | + | + | | | 1289 |
| 1 | Soaked flour | HPLC | + | + | | | | | 1241 |
| 2 | Seed[b] | HPLC | | | 0 | 0.12-0.17 | 1.49-1.36 | 8.82-6.48 | 1327 |
| *Samanea saman* Merr. (Rain Tree) | | | | | | | | | |
| 1 | Pulvini | $^3$H-Ins | + | + | + | | | | 1219 |
| *Secale cereale* L. (Oats) | | | | | | | | | |
| 3 | Grain | HPLC | | | 0 | 0 | 0 | 4.18-8.97 | 1328 |
| *Sorghum bicolor* (L.) Moench (Sorghum) | | | | | | | | | |
| 2 | Grain | HPLC | | | 0 | 0 | 0-0.54 | 8.77-9.68 | 1328 |
| *Spirodela polyrhiza* (L.) Schleid. (Giant Duckweed) | | | | | | | | | |
| 1 | Axenic culture | $^3$H-Ins | + | + | + | + | + | + | 1243 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Theobroma cacao* L. (Cocoa) | | | | | | | | | |
| 1 | Husk | HPLC | | | 0 | 0 | 0 | 0.28[c] | 1126 |
| *Triticum aestivum* L. (Wheat) | | | | | | | | | |
| 10 | Grain | HPLC | | | 0 | 0 | 0 | 4.90-9.27 | 1328 |
| 1 | Bran | HPLC | | | 0 | 1.24 | 6.92 | 39.47 | 1328 |
| 1 | Ear stalk | $^{32}P_i$ | + | | | | | | 1242 |
| *Vallisneria* spp. (Eelgrass) | | | | | | | | | |
| 1 | Whole plant[a] | IEC | | | 0.068 | | + | | 912 |
| *Vicia faba* L. (Broad or Faba Bean) | | | | | | | | | |
| 2 | Bean[c] | HPLC | | | 0.016-0.020 | 0.043-0.047 | 0.075-0.212 | 0.345-0.885 | 922 |
| *Vicia faba* L. ssp. *minor* L. (Small Horsebean) | | | | | | | | | |
| 1 | Bean[a] | HPLC | | | | | 0.14 | 17.45 | 1333 |
| *Vigna radiata* (L.) Wilcz. (Mung Bean) | | | | | | | | | |
| 1 | Seed[a] | IEC | | 0.08 | 0.19 | 0.39 | 0.69 | | 1335 |
| 1 | Sprout | $^{32}P_i$ | | | | | + | | 1320 |
| *Vigna unguiculata* (L.) Walp. (Cowpea) | | | | | | | | | |
| 1 | Seed | HPLC | | | 0.01 | 0.26 | 2.52 | 12.6 | 1327 |
| *Zea mays* L. (Corn) | | | | | | | | | |
| 1 | Seed | IEC | | | | + | + | | 1216 |
| 2 | Grain | HPLC | | | 0 | 0 | 0.22-0.32 | 7.29-11.43 | 1328 |
| 1 | 1-week seedling | IEC | + | + | + | + | + | | 1216 |
| 1 | Root, apical segment | IEC | ++ | + | + | | | | 1336 |

*nmol/g fresh weight basis unless stated otherwise.
[a]μmol/g.
[b]mg/g.
[c]Percent of plant tissue.
[d]Percent of total P.

# Glyceroinositol Phosphates

This group comprises monoglyceryl esters of three *myo*-inositol phosphates:




**GroPIns**, R = R′ = H
**GroPInsP**, R = P(O)$(OH)_2$, R′ = H
**GroPInsP$_2$**, R = R′ = P(O)$(OH)_2$

Glycerophosphoinositol (GroPIns), $C_9H_{19}O_{11}P$; Beilstein **6**, $E_{III}$ 6933, $E_{IV}$ 7925. D-*myo-Inositol 1-(R-2,3-Dihydroxypropyl Hydrogen Phosphate)* [1958].

Glycerophosphoinositol 4-Phosphate (GroPInsP), $C_9H_{20}O_{14}P_2$; Beilstein **6**, $E_{III}$ 6934. D-*myo-Inositol 4-(Dihydrogen Phosphate) 1-(R-2,3-Dihydroxypropyl Hydrogen Phosphate)* [1961].

Glycerophosphoinositol 4,5-Bisphosphate (GroPInsP$_2$), $C_9H_{21}O_{17}P$; Beilstein **6**, $E_{III}$ 6934. D-*myo-Inositol 4,5-Bis(Dihydrogen Phosphate) 1-(R-2,3-Dihydroxypropyl Hydrogen Phosphate)* [1961].

## Occurrence

The presence of these compounds in the higher plants has not been rigorously established, but they are included here as they are likely products of the action of phospholipase $A_1$ and $A_2$ on PI, PIP, and $PIP_2$, all of which (including the enzymes) are known to occur in higher plants. Heim and Wagner[1200] identified GroPIns, GroPIns(4)P, and GroPIns(4,5)$P_2$ in Madagascar periwinkle and tobacco culture cell extracts by their retention times on HPLC. Brearly and Hanke[1338] identified GroPIns(3)P and GroPIns(3,4)$P_2$ in addition to the 4- and 4,5-analogs as products of deacylation of $PIP_2$ in *Spirodela polyrrhiza*. All the other compounds listed in Fig. 3-6 were prepared from the corresponding inositol phosphatides by base-catalyzed methanolysis.[1203]

## Physical Properties

### Glycerophosphoinositol

GroPIns [R.N. 129830-95-1; see also 2816-11-7, 27082-28-6, 37449-91-5, and 40529-46-2]: $[\alpha]_D^{20}$ −18° ($H_2O$).[1339] Spectra: GC/MS (fig.),[1340] $^{31}$P NMR.[68,1341] Chromatography: PC,[1339] TLC,[1266] IEC,[1207] GC,[123] HPLC.[1268]

$C_6H_{11}NH_3.C_9H_{18}O_{11}P$: Crystals from alcohol, $[\alpha]_D^{25}$ −14.0° ($H_2O$).[1207] *Hemihydrate*: mp 124-127 °C dec., $[\alpha]_D^{20}$ −13.2° ($H_2O$).[1247] Spectra: IR.[1247] Chromatography: PC.[1247]

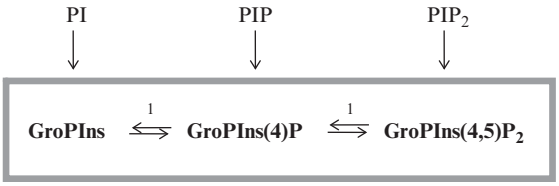



**FIGURE 3-6 Glycerophosphoinositols**. (1) Alkaline phosphatase [E.C. 3.1.3.1].[1205]

### Glycerophosphoinositol 4-Phosphate

GroPInsP [R.N. 129830-96-2; see also 29595-51-5 and 77055-41-5]: $[\alpha]_D$ −4.8° (acid solution), −5.5° (basic solution)[1342]; p$K_a$ 5.99.[1343] Spectra: GC/MS (fig.).[1340] Chromatography: PC,[1342] IEC,[1342] GC,[123] HPLC.[1268] Ca(II), Mg(II), Ni(II) complexes: Stability constants.[1343]

### Glycerophosphoinositol 4,5-Bisphosphate

GroPInsP$_2$ [R.N. 111188-72-8; see also 92216-46-1 and 94161-15-6]: $[\alpha]_D$ −1.1° (acid solution), −3.3° (basic solution)[1342]; p$K_a$ 5.70, 8.05.[1344] Spectra: GC/MS (fig.).[1340] Chromatography: PC,[1342] IEC,[1342] HPLC.[1268] Ca(II), Mg(II), Ni(II) complexes: Stability constants.[1343,1344]

## Synthesis

None of the naturally occurring compounds have been synthesized. DL-GroPIns has been prepared by the reaction of DL-*myo*-inositol 1-phosphate with glycidol.[1345]

## Hydrolysis

Hydrolysis of DL-GroPIns with 1*N* NaOH for 30 min at 60 °C yields a 65:35 mixture of glyceryl phosphate and *myo*-inositol phosphate in addition to glycerol and *myo*-inositol (but no $P_i$). PC shows that both phosphates are partly isomerized, the ratios being 44:56 for Gro(1)P:Gro(2)P and 70:30 for Ins(1)P:Ins(2)P.[1345] Similarly, hydrolysis of GroPInsP or GroPInsP$_2$ with 1*N* NaOH at 100 °C yields a mixture of glyceryl phosphate and InsP$_2$ (48:52) or InsP$_3$ (26:74), respectively, both partially isomerized (ratios not determined).[1205]

Hydrolysis of GroPInsP or GroPInsP$_2$ with bacterial phosphatase at pH 8.2 and 40 °C cleaves only the primary phosphate groups giving GroPIns and $P_i$.[1205]

## Extraction and Separation

The three GroPIns's can be isolated from plant tissue by extraction with $CHCl_3$/methanol (1:2) containing 1% HCl and separated from the InsP's by IEC or HPLC.[1200] In most cases, however, they are prepared from the corresponding phosphatidylinositol (PI, PIP, or PIP$_2$) by base-catalyzed methanolysis and separated from each other by IEC, HPLC, PE,[1204] or 2d-PC.[1203] The IEC separation may be performed on a Dowex-1 column with 0 → 0.4*M* LiCl gradient elution[1342] and the HPLC separation on a Partisil-10 SAX anion exchange column with 0 → 1.0*M* ammonium formate gradient at pH 3.7[1201] or a Supelco LC-8

reversed-phase column with $0 \rightarrow 0.8M$ $KH_2PO_4/n$-propanol gradient containing a surfactant, hexadecyltrimethylammonium hydroxide.[1346] The order of elution is GroPIns > GroPInsP > GroPInsP$_2$ in all four methods (Table 3-5).

**Table 3-5** Glyceroinositol Phosphates in Plants*

| No. | Plant part | | GroPIns | GroPInsP | GroPInsP$_2$ | References |
|---|---|---|---|---|---|---|
| *Brassica oleracea* L. var. *botrytis* (Cauliflower) | | | | | | |
| 1 | Callus | IEC | + | + | + | 1199 |
| 1 | Hypocotyl | IEC | + | + | + | 1199 |
| *Catharanthus roseus* (L.) G. Don (Madagascar Periwinkle) | | | | | | |
| 1 | Cell suspension culture | IEC | 8.5 | | | 1200 |
| 1 | Cell suspension culture | HPLC | + | + | | 1200 |
| *Daucus carota* L. (Carrot) | | | | | | |
| 1 | Culture cells | HPLC | | | + | 1201 |
| *Dianthus caryophyllus* L. (Carnation) | | | | | | |
| 1 | Flower petal | HPLC | + | + | | 1202 |
| *Hordeum vulgare* L. (Barley) | | | | | | |
| 1 | Leaf[a] | PC/PC | + | | | 1203 |
| 1 | Aleurone layer[b] | PE | + | + | + | 1204 |
| *Nicotiana tabacum* L. (Tobacco) | | | | | | |
| 1 | Leaf [a] | PC/PC | + | | | 1203 |
| 1 | Culture cells | HPLC | + | + | + | 1200 |
| *Pisum sativum* L. (Peas) | | | | | | |
| 1 | Leaf, 12 days old | HPLC | | + | + | 1201 |
| *Spirodela polyrrhiza* (L.) Schleid. (Giany Duckweed) | | | | | | |
| 1 | Whole plant | HPLC | + | + | + | 1205 |
| *Trifolium repens* L. (White Clover) | | | | | | |
| 1 | Leaf | PC/PC | + | | | 1203 |
| *Triticum aestivum* L. (Wheat) | | | | | | |
| 1 | Flour [a] | PC/PC | + | | | 1206 |
| *Zea mays* L. (Corn) | | | | | | |
| 1 | –[a] | IEC | + | | | 1207 |

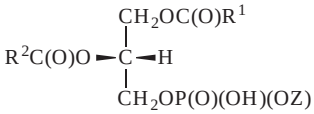
*nmol/g fresh weight basis unless stated otherwise.

[a]Species not given.

[b]Ratio of GroPIns:GroPInsP:GroPInsP$_2$ is 100:0.5:0.1.

# 4 Phospholipids

This group comprises the phospholipids PC, PE, PG, PI, PS, PA, and DPG, and the phospholipid derivatives PIP, $PIP_2$, and NAPE:



| PL | ZOH component | $RCO_2H$ component | |
|---|---|---|---|
| PA | H | 16:0 | Palmitic acid |
| PC | Choline | 18:0 | Stearic acid |
| PE | Ethanolamine | 18:1 | Oleic acid |
| PG | Glycerol | 18:2 | Linoleic acid |
| PS | L-Serine | 18:3 | Linolenic acid |
| PI | *myo*-Inositol | and other long-chain fatty | |
| PIP | *myo*-Inositol 4-phosphate | acids in various combinations | |
| $PIP_2$ | *myo*-Inositol 4,5-bisphosphate | | |
| DPG | PA | | |
| NAPE | *N*-Acylethanolamine | | |

The plant phospholipids are all esters of phosphatidic acid (PA, Z = H). These esters are commonly called phosphatidylcholine (PC), phosphatidylethanolamine (PE), and so on, names that are adequate for this part of the chapter, which treats the phospholipids in a general way. A different nomenclature is introduced later in this chapter that enables individual members of each phospholipid class to be identified unambiguously.

For general references on the phospholipids, see Butt and Beevers,[1347] Kates,[1348] Kates,[1349] Stumpf,[1350] Moore,[1351] Coté and Crain,[1352] or Cevc.[4297]

## Occurrence

The occurrence of lecithin in plant seeds was first reported by Schulze and Steiger[1353] in 1889. Its identity as phosphatidylcholine (PC) was established in a series of research studies by Schulze's group over a 20-year period. Phosphatidylethanolamine (PE) was detected in soybeans in 1925, but the "cephalin" fraction that contained it was later shown to also contain *myo*-inositol[1354] and serine[1355] residues, among others. The situation was not clarified until the advent of chromatographic methods for their separation in the 1950s. The number of phospholipid classes then expanded rapidly with the discovery of PI (1957) in runner beans,[1356] PG (1958) in tobacco,[1203] DPG (1960) in corn and clover,[1357] NAPE (1965) in wheat,[1358] and PIP and $PIP_2$ (1985) in wild carrot.[1359] All of these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phospholipids are now known to be normal constituents of the higher plants as well as of animals and lower plants, but they are not all present in all plant tissues nor in all plant tissues at different stages of development.

The metabolic pathways for the biosynthesis of the phospholipids are outlined in Fig. 4-1. The key precursor for all of the phospholipids is phosphatidic acid (PA), formed from *sn*-glycero-3-phosphate (α-GP) by acylation with acyl-CoA (step 1). The phospholipids are seen to be split into two groups depending on which metabolite is activated by cytidine triphosphate (CTP). In one pathway, phosphocholine and phosphoethanolamine are activated by CTP forming CDP-choline and CDP-ethanolamine, respectively, which then react with diacylglycerol (DG ), formed from PA by hydrolysis with phosphatase (step 2), giving PC (step 4) or PE (step 5). In the other pathway, the phosphate group of PA is activated by CTP giving cytidine diphosphate-diacylglycerol (CDP-DG, step 3), which then reacts with L-serine, *myo*-inositol, or α-GP giving PS (step 6), PI (step 7), or PG (step 8a), respectively. Interconversion of PE and PS can occur by exchange of PE with L-serine (step 9) or by decarboxylation of PS (step 10). NAPE is formed from PE in seed microsomes (step 11) by acylation.[1361] PIP and $PIP_2$ are formed from PI by successive phosphorylation with ATP (steps 12 and 13).[1362] DPG is formed from PG in plant mitochondria (step 14) by reaction with CDP-DG.[1363]

## Stereochemistry

The phospholipids all contain a chiral center at the $C_2$ position of the glyceryl moiety and are therefore capable of existing in two configurations, which by convention are labeled R and S. All naturally occurring plant phospholipids have the R configuration, as illustrated later, and can therefore display optical activity. Some examples are given in Table 4-1.

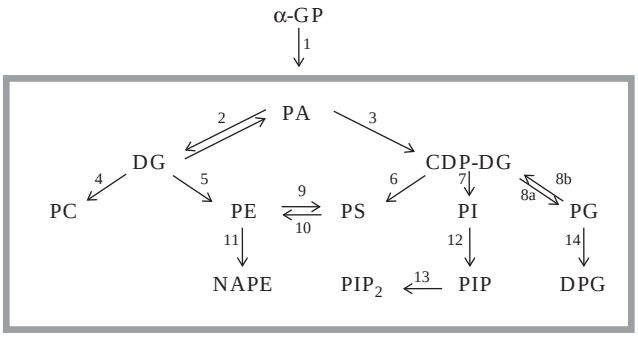
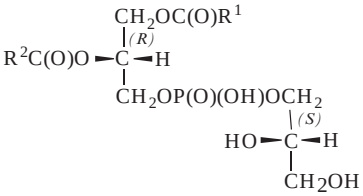



**FIGURE 4-1 Phospholipid Metabolism**. (1) Acyl-CoA:*sn*-glycerol-3-phosphate 1-*O*-acyltransferase [E.C. 2.3.1.15]. (2) 3-*sn*-Phosphatidate phosphohydrolase [E.C. 3.1.3.4]. (3) CTP:Phosphatidate cytidylyltransferase [E.C. 2.7.7.41], Mn(II). (4) CDP-Choline:-DG cholinephosphotransferase [E.C. 2.7.8.2], Mg(II). (5) CDP-Ethanolamine:DG ethanolaminephosphotransferase [E.C. 2.7.8.1], Mg(II). (6) CDP-DG:L-serine 3-*O*-phosphatidyltransferase [E.C. 2.7.8.8], Mn (II). (7) CDP-DG:*myo*-Inositol 3-phosphatidyltransferase [E.C. 2.7.8.11], Mn(II). (8a) CDP-DG:*sn*-glycerol 3-phosphate 3-phosphatidyltransferase [E.C. 2.7.8.5]. (8b) Phosphatidylglycerophosphate phosphohydrolase [E.C. 3.1.3.27]. (11) Phosphatidylethanolamine *N*-acyltransferase.[1360]

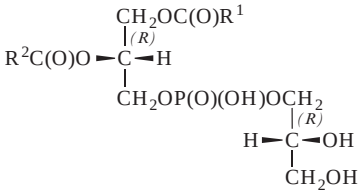
**Table 4-1** Physical Properties of Some Plant Phospholipids

| | |
|---|---|
| *Arachis hypogaea* L. (Peanut), seed | |
| PI | Ba pptn. sodium salt: crystalline solid[1364] |
| *Beta vulgaris* L. (sugarbeet), tuber | |
| PG | $^{13}$C NMR (fig.)[1365] |
| *Glycine max* (L.) Merr. (soybean), bean | |
| PC | $^{31}$P NMR (fig.),[1366] TGA.[1367] Prep. HPLC, FT-IR (fig.)[1368] |
| PE | $^{31}$P NMR (fig.),[1366] TGA.[1367] |
| PI | $^{31}$P NMR (fig.),[1366] FAB-MS (fig.),[1369] FTICR-MS/MS.[1370] DEAE cellulose and silicic acid chromatography, IR (fig.), PC, TLC.[1371] Ammonium salt (1:1): powder, $[\alpha]_D^{27}$ +6.0° ($CHCl_3$), silicic acid column chromatography.[1372] Na salt (1:1); small colorless needles[1372] |
| PA | $^{31}$P NMR (fig.)[1366] |
| NAPE | Triethylamine salt: light pale viscous oil, $[\alpha]_D^{22}$ +4.7° ($CHCl_3$), IR, TLC[1373] |
| LPC, LPE, LPI, LPA | $^{31}$P NMR (fig.)[1366] |
| *Gossypium hirsutum* L. (Cotton), seed kernel | |
| PC | $[\alpha]_D$ +7.7° ($CHCl_3$), IR, prep. TLC[1374] |
| PE | $[\alpha]_D$ +6.1° ($CHCl_3$), IR, prep. TLC[1374] |
| PI | $[\alpha]_D$ +3° ($CHCl_3$),[2403] IR, prep. TLC[1374] |
| *Helianthus annuus* L. (Sunflower), seed kernel | |
| PC | Light yellow rubberlike substance, prep. TLC,[1375] $[\alpha]_D^{27}$ +7.45° ($CHCl_3$), IR[1376] |
| PE | Light yellow waxy substance, prep. TLC,[1375] $[\alpha]_D^{27}$ +6.1° ($CHCl_3$), IR[1376] |
| PI | Almost colorless pulverulent substance, prep. TLC,[1375] $[\alpha]_D^{27}$ +9.7° ($CHCl_3$), IR[1376] |
| PA | Prep. TLC,[1375] IR[1376] |
| *Hibiscus cannabinus* L. (Kenaf), seed kernel | |
| PC | $[\alpha]_D^{20}$ +6.3° ($CHCl_3$), prep. TLC[1377] |
| *Oryza sativa* L. (Rice), polished grain | |
| LPC | $CdCl_2$ pptn., colorless needles, s. ~100 °C, dec. 262-264° C with gassing, $[\alpha]_D^{20}$ −4.52° ($CHCl_3$), sol. water, methanol, ethanol, glacial acetic acid, $CHCl_3$, pyridine, insol. ether, petr. ether, acetone. Aqueous solution, neutral with an irritating astringent taste; poisonous[1378] |
| *Spinacia oleracea* L. (Spinach), leaf | |
| PC | IR (fig.), DEAE cellulose column chromatography, countercurrent distribution[1379] |
| PE | IR (fig.), DEAE cellulose column chromatography, countercurrent distribution[1379] |
| PG | IR (fig.), DEAE cellulose column chromatography, countercurrent distribution.[1379] Ammonium salt: $[\alpha]_D^{25}$ +1.0° ($CHCl_3$)[1380] |
| PI | IR (fig.), DEAE cellulose column chromatography, countercurrent distribution[1379] |
| *Triticum aestivum* L. (Wheat), seed germ | |
| PI | Ba pptn., insol. ethanol. Sodium salt: White needles, mp 145 °C (s. 125-130 °C), sol. $CHCl_3$, $CCl_4$, benzene, slightly sol. methanol, insol. ether, petr. ether, acetone; viscous colloidal dispersion in water[1109]; photoelectron spectrum (fig.)[1381] |
| PA | Monopotassium salt: $[\alpha]_D^{20}$ +9.4° ($CH_3OH$), very sol. ether, $CHCl_3$, sol. methanol (~2%), insol. ethanol; PC, TLC[1382] |
| DPG | Oil, very sol. ethanol; PC, TLC. Na salt: solid, slightly sol. ethanol. Ba salt, gelatinous soln.in dry ether[1383] |
| *Vigna mungo* (L.) Hep. (Black gram), seed | |
| NAPE | IR (fig.), TLC, HPTLC[1384] |
| NALPE | IR (fig.), TLC, HPTLC[1384] |

The phosphatidylglycerols (PG) contain two such chiral centers, one in each glycerol moiety, and are therefore capable of existing in four configurations, which by convention are labeled *R*,*S*; *R*,*R*; *S*,*R*; and *S*,*S*. In recent work in which the stereoisomers were separated by chiral-phase HPLC, the PG from cabbage leaf and soybean was found to consist solely of R,S isomers, whereas those of *Escherichia coli* and egg yolk consisted of 89:11% and 45:55% mixtures of R,S and R,R isomers, respectively[1385]:



*R*,*S* (plant, microbial, animal)



*R*,*R* (microbial, animal)

## Physical Properties

Physical properties have been reported for a few phospholipids derived from plant sources without regard to the presence therein of acyl groups of different chain lengths or degrees of unsaturation. Some of these are given in Table 4-1.

## Extraction

The most widely used procedures for the extraction of lipids are those of Folch *et al.*[1386] and Bligh and Dyer,[1387] modified for use with plant tissues. Both procedures employ chloroform-methanol (2:1 or 1:1) solvent mixtures, followed by backwashing with water or salt solution to remove nonlipid contaminants. A preliminary heat treatment with boiling water, boiling 2-propanol[1356] or the like is recommended to inactivate enzymes such as phospholipase D, which can hydrolyze phospholipids to phosphatidic acid or react with methanol to form phosphatidylmethanol as an unwanted artifact.[1388,1389]

> *For quantitative analyses of the constituent phospholipids, weighed amounts of cotyledons or seed coats were steamed for 15 min prior to comminution in 20 vol of chloroform-methanol (C/M 2:1, v/v) using a Polytron PT 20 homogenizer (Kinematica, Lucerne, Switzerland). Filtrates from these homogenates were partitioned against 0.2 vol of 0.9 % (w/v) NaCl . . . . Filtered homogenates plus washings were brought to 2:1 (v/v) or 1:1 (v/v) with respect to chloroform and methanol and were washed according to Folch* et al.[1386] *and Bligh and Dyer,*[1387] *respectively. Washed lipid extracts were dried on a rotary evaporator and the dry lipid redissolved in chloroform so that 1 ml of lipid solution was equivalent to 1 g fresh weight of cotyledons.*
>
> Roughan, P. G.; Slack, C. R.; Holland, R., "Generation of Phospholipid Artefacts during Extraction of Developing Soybean Seeds with Methanolic Solvents", *Lipids* **1978**, *13*(7), 497–503,[1388] reprinted by permission of Springer, © 1978.

The combined lipids may be subjected to further purification by column chromatography on Sephadex G-25, which removes any carbohydrate or protein that may have coextracted with the lipid,[1390] or by thin-layer chromatography on silica gel, which removes any pigments that may be present.[1391] In some cases, more vigorous conditions are required. Lipids of seed tissues such as wheat bran, embryo, or whole grain, for example, are extracted more efficiently by boiling water-saturated n-butanol than by methanol/chloroform or 2-propanol/chloroform.[1392,1393] Supercritical fluid extraction of oilseeds with $CO_2$ has received much attention in recent years because the extract is free of solvent and low in free fatty acids or pigments. It can be applied to the extraction of phospholipids if a cosolvent is used (such as ethanol) because the phospholipids are not soluble in neat $CO_2$.[1394,1395]

## Separation and Analysis

Plant tissues, in contrast to animal or microbial tissues, tend to have much lower amounts of phospholipids in relation to neutral or nonpolar lipids. For this reason, it is usually advisable to do a preliminary fractionation to remove the bulk of the nonpolar lipids from the extract. A widely used procedure is column chromatography on silicic acid. Successive elution with chloroform, acetone, and then methanol separates the lipid extract into neutral lipids, glycolipids, and phospholipids, respectively. Some of the PA and DPG, however, may be carried into the acetone fraction.[1349a]

> *The lipid preparations, dissolved in diethyl ether, were applied to columns of Mallinckrodt silicic acid (250 parts by weight; activated at 110° overnight) and the "neutral" lipids (hydrocarbons, sterol esters, triglycerides, free fatty acids, diglycerides and sterols) and most of the pigments were eluted with diethyl ether. Polar lipids (glycolipids, phospholipids, sterol glycosides) and residual pigment were then displaced with ether-methanol (1:1, v/v) and methanol. Positive $N_2$ pressure was generally applied to the columns and the separation of neutral and polar lipids from a total of about 250 mg lipid took less than 3 h.*
>
> Nichols, B. W., "Separation of the Lipids of Photosynthetic Tissues: Improvements in Analysis by Thin-Layer Chromatography", *Biochim. Biophys. Acta* **1963**, *70*(4), 417–422,[1396] reprinted by permission of Elsevier, © 1963.

Older methods that are now seldom used are acetone precipitation,[1349b] dialysis,[1397] countercurrent distribution,[1379] and the use of other column supports such as DEAE cellulose,[1379] Sephadex LH-20,[1398] or alumina.

### *(1) Thin-Layer Chromatography (TLC) Method*

Two-dimensional TLC has been the method of choice for the separation and quantitation of plant phospholipids since the early 1960s. The $R_f$ values for the major phospholipids (PL) and lysophospholipids (LPL) are given in Table 4-2.

**Table 4-2** Separation of Phospholipid Classes by TLC [1393]

| | Dimension | | | Dimension | |
|---|---|---|---|---|---|
| **PL** | **1st** | **2nd** | **LPL** | **1st** | **2nd** |
| PC | 0.37 | 0.28 | LPC | 0.13 | 0.09 |
| PE | 0.49 | 0.59 | LPE | 0.19 | 0.34 |
| PG | 0.46 | 0.71 | | | |
| PI | 0.09 | 0.39 | | | |
| PS | 0.19 | 0.34 | | | |
| PA | 0.01 | 0.77 | | | |
| DPG | 0.50 | 0.86 | | | |
| NAPE | 0.84 | 0.96 | NALPE | 0.66 | 0.82 |

*The polar lipid fraction [from a lipid extract of soft winter wheat grain after silicic acid column chromatography] was evaporated to dryness under $N_2$ and redissolved in a small vol. of $CHCl_3$. Separation of the polar lipids into classes was achieved by 2-D TLC on Si gel G [using] $CHCl_3$-MeOH-ammonia (30 %, w/v) (13:5:1) for the 1st dimension and $CHCl_3$-$Me_2CO$-MeOH-HOAc-$H_2O$ (6:8:2:2:1) for the 2nd dimension. The 1st solvent was removed under vac. Atm pres was reinstated with $N_2$ and chromatograms were immediately run in the 2nd solvent. Chromatograms were then dried in air and the spots were detected using $I_2$ vapour . . . Phospholipids were tentatively identified by comparing their TLC $R_f$ values with published data, by co-chromatography with authentic samples, and by their behaviour with various spray reagents. For the latter purpose, the developed chromatograms were sprayed with 0.3 % ninhydrin–5 % lutidine in $H_2O$ satd. n-BuOH for amino groups, a modified Dragendorff reagent for choline, and a modified Zinzadze reagent for phosphate. The use of 0.6 % $K_2Cr_2O_7$ in 55 % $H_2SO_4$ as a general detection reagent also allowed the identification of some nonphosphorus polar lipids. The quantities of individual phospholipids were determined [as follows]. Chromatogram spots that had been located using $I_2$ vapour and Si gel blanks were aspired directly into 50 ml Kjeldahl flasks containing a liquid trap of 0.7 ml 70 % $HClO_4$. The contents of the flask were refluxed at 200° until clear and then cooled. 3.3 ml $H_2O$, 0.5 ml 2.5 % ammonium molybdate, and 0.5 ml 10 % ascorbic acid were then added. The mixture was transferred to a reductase tube, and heated for 5 min. at 100°. After cooling, the Si gel was removed by a brief centrifugation and the A at 800 nm of the supernatant was measured.*

Colborne, A. J.; Laidman, D. L., "The Extraction and Analysis of Wheat Phospholipids", *Phytochemistry* **1975**, *14*(12), 2639–2645,[1393] reprinted by permission of Elsevier, © 1975.

The reproducibility of the method was tested in a seven-laboratory collaborative study.[1399] The method was later adopted as an AOCS standard for phospholipids in animal or vegetable lecithins.[1400] Some other methods that have been employed for the quantitation of the phospholipid classes after TLC include (a) photodensitometry after charring with 50% $H_2SO_4$, cupric acetate, and the like, (b) automated scanning densitometry,[1401]

(c) scintillation counting for PLs labeled with [$^3$H],[1402] [$^{14}$C],[1403] or [$^{32}$P],[1389] (d) measurement of the absorbance at 720 nm after spraying with the Dittmer-Lester reagent,[1404] and (e) fluorescence detection.[1405] Automation of the TLC method is possible with the use of Chromarods in the Iatroscan TLC/FID system.[1406]

### *(2) High-Performance Liquid Chromatography (HPLC) Method*

The HPLC method, introduced in 1981,[1407,1408] has become a useful alternative to TLC for the separation and quantitation of plant phospholipids. With few exceptions, the column packing is silica gel (5μ Porasil, LiChrosorb Si-60, etc.) and the mobile phase is *n*-hexane/2-propanol/water or acetonitrile/methanol/water. The order of elution is PE > PG > PI > PA > PS > PC with the former[1407] and PI > PS > PE > PC with the latter,[1368] but it can deviate considerably with changes in solvent ratios or gradients. In most cases, the phospholipids are detected by UV absorption at 206 nm and quantitated by phosphorus analysis,[1407] which can be brought online by means of an automatic phosphorus analyzer,[1409] or by transmethylation with MeOH/NaOMe and GC analysis of the FAME,[1410] as described later in this chapter. The reproducibility of the method for analysis of phospholipids in commercial soybean lecithin has been tested in two multilaboratory collaborative studies.[1411,1412]

> *The lipid sample was filtered through a 0.4μm pore size polycarbonate membrane . . .; the solvent was evaporated with a stream of nitrogen gas, and the sample was dissolved in 0.5 mL of chloroform. An aliquot containing ∼1 mg of phospholipid was injected into the HPLC. Liquid chromatographic analysis was performed with a Waters' Associates liquid chromatograph [consisting of] two Model 6000A solvent pumps . . . a Model 660 solvent programmer for gradient elution . . . a U6K injector . . . a 30 cm × 3.9 mm Porasil column . . . packed with 10 μm diameter silica gel particles was used. The solvent system selected was a mixture of hexane, 2-propanol, and water. . . . Solvent composition was initially . . . 6:8:0.5 v/v/v. A linear increase in the water content during a 25-min period resulted in a final solvent composition of 6:8:1.5. Solvent flow was maintained at 1.5 mL/min. Detection of eluting components was by absorbance at 206 nm . . . . The phosphorus content of the fractions collected from the HPLC was determined by using Bartlett's modification (Bartlett, 1959) of the Fiske-SubbaRow method (Fiske and SubbaRow, 1925).*
>
> Reprinted with permission from Ashworth, E. N.; St. John, J. B.; Christiansen, M. N.; Patterson, G. W., "Characterization of the Phospholipid Composition of Wheat Roots Using High-Performance Liquid Chromatography", *J. Agric. Food Chem.* **1981**, *29*(4), 879–881,[1407]
> © American Chemical Society.

Direct quantitation of the phospholipids is possible if the UV detection is replaced by flame ionization (FID)[1413] or evaporative light scattering (ELS)[1414] detection. Other methods of detection that have been proposed are FTIR,[1368] plasmaspray ionization MS,[1415] and postcolumn derivatization.[1416]

Moreau *et al.*[1413] developed a protocol that separates all seven of the major phospholipids—DPG, PE, PG, PI, PA, PS, and PG—in order of elution as well as LPC in one 60-min run using a Lichrosorb Si-60 column and FID detection. NAPE and NALPE can be separated from each other and from other phospholipids by HPLC on Lichrosorb Si-60 with ELS detection.[1417] The phosphoinositides PI, PIP, and $PIP_2$ can be separated by HPLC on an amino-NP silica column with liquid scintillation detection.[1418]

Methods have been developed for the preparation of gram-scale quantities of PC, PE, and PI of high purity (>99%) from soybean lecithin using preparative HPLC columns of 4.6- to 50-mm inner diameter.[1419,1420] Flash chromatography of rapeseed lecithin also provides gram-scale separation of PC, PE, and PI. but only the PC is 99% pure.[1421]

The normal-phase HPLC procedures described here serve to separate the phospholipids by class. Later we shall see that the phospholipids of each class can be further separated into their component molecular species by reversed-phase HPLC.

#### *(3) Micellar Electrokinetic Chromatography (MEKC) Method*

This method, which is still in the developmental stage, provides an alternative to HPLC that has the advantage of much higher peak capacity resulting in improved resolution. It separates the phospholipids based on their partition coefficients between a mobile phase and a pseudostationary micellar phase. The mobile phase is usually 30% *n*-propanol and the micellar phase a buffered solution of cholic acid[1422] or deoxycholic acid.[1423] The method has been applied to commercial soybean and rapeseed lecithins.[1422,1423]

### Analysis Without Separation

#### *(1) $^{31}P$ Nuclear Magnetic Resonance (NMR) Method*

This method, adopted in 1988, is useful in that it quantitates phospholipids directly by their phosphorus content. A crude soybean extract was separated into 11 phospholipid classes (7 PLs and 4 LPLs) in a single 24-h run.[1366] The $^{31}P$ chemical shift $\delta$ for each phospholipid (PL) and lysophospholipid (LPL) class is given in Table 4-3.

For example, seven phospholipid classes and four lysophospholipid classes were identified in a crude soybean extract in a single 24-h run.[1366]

**Table 4-3** $^{31}P$ NMR of Phospholipid Classes[1366]

| PL | δ | LPL | δ |
|---|---|---|---|
| PC | −0.84 | LPC | −0.28 |
| PE | −0.01 | LPE | 0.43 |
| PG | 0.52 | LPG | 1.09 |
| PI | −0.37 | LPI | 0.10 |
| PA | 0.25 | LPA | 0.83 |
| DPG | 0.18 | | |

## Fatty Acid Distribution

Each class of phospholipid in a typical plant extract comprises long-chain fatty acids of variable chain lengths and degrees of unsaturation. The distribution of fatty acid residues within each class is readily determined by transesterification with methanol and analysis of the resulting mixture of fatty acid methyl esters (FAME) by gas chromatography. The following procedure is typical:

> *Bands were scraped off [the TLC plates] on to small chromatographic columns from which the . . . phospholipids [were eluted] with methanol containing 5 per cent. of anhydrous hydrogen chloride; 1 ml of the standard solution of methyl heptadecanoate was added to each fraction . . . . The phospholipids [were] transesterified by refluxing for 2 hours in the methanolic hydrogen chloride . . . . Methyl esters were dissolved in hexane for . . . gas liquid chromatographic analyses [which] were carried out on columns of 15 per cent w/v poly(ethyleneglycol adipate) on Chromosorb W . . . in a Pye 104 chromatograph. The amount of each ester present (per cent w/w) was calculated from the product of the peak height and retention time, and results obtained were converted into mole per cent . . . .*
>
> Christie, W. W.; Noble, R. C.; Moore, J. H., "Determination of Lipid Classes by a Gas Chromatographic Procedure", *Analyst* **1970**, *95*(11), 940–944,[1424] reproduced by permission of the Royal Society of Chemistry, © 1970.

Morrison *et al.*[1425] have provided a list of factors that can be used to convert % P or % FAME to % phospholipid or % lysophospholipid (Table 4-4):

The FAME method has been applied to the majority of the phospholipids listed in Table 4-15. The transesterification is often carried out with acidic catalysts such as anhydrous HCl or sulfuric acid or with basic catalysts such as sodium methoxide or anhydrous potassium hydroxide; see Hammond[2091] for a discussion of the relative merits of each method.

**Table 4-4** Conversion Factors for FAME

| PL | Factor | | LPL | Factor | |
|---|---|---|---|---|---|
| | P[a] | FAME[b] | | P[a] | FAME[b] |
| PC | 24.60 | 1.33 | LPC | 16.47 | 1.79 |
| PE | 23.22 | 1.26 | LPE | 15.08 | 1.64 |
| PG | 24.22 | 1.31 | LPG | 16.08 | 1.74 |
| PI | 27.09 | 1.48 | LPI | 18.95 | 2.05 |
| PS | 24.67 | 1.34 | LPS | 16.53 | 1.79 |
| PA | 21.83 | 1.18 | | | |
| DPG | 22.75 | 1.23 | | | |
| NAPE | 31.35 | 1.70 | NALPE | 23.22 | 2.52 |

[a]Weight P × factor = weight PL or LPL.
[b]Weight FAME × factor = weight PL or LPL.

**Table 4-5** Fatty Acid Groups in Tomato Leaf PG (mol%)[2092]

| | Acyl Group | Composition | Distribution | |
|---|---|---|---|---|
| | | | $C_1$ | $C_2$ |
| 16:0 | Palmitoyl | 17 | 9 | 8 |
| 16:1 | *trans*-Hexadecenoyl | 37 | 0 | 37 |
| 18:0 | Stearoyl | 1 | 1 | 0 |
| 18:1 | Oleoyl | 4 | 4 | 0 |
| 18:2 | Linoleoyl | 23 | 19 | 4 |
| 18:3 | Linolenoyl | *18* | *16* | *2* |
| | | 100 | 49 | 51 |

Table 4-5 illustrates the method as applied to tomato leaf phosphatidylglycerol.[2092] The predominant fatty acids are *trans*-hexadecenoic acid, located exclusively on $C_2$; linoleic acid and linolenic acid, located mainly on $C_1$; and palmitic acid, evenly divided between $C_1$ and $C_2$. The distribution between $C_1$ and $C_2$ was determined by separate experiments in which the PG was hydrolyzed by lipase from the mold *Rhizopus delemar*, which cleaves the $C_1$ acyl group selectively. From these results it can be inferred that the main molecular species in tomato leaf PG are 1-linoleoyl- and 1-linolenoyl-2-*trans*-hexadecenoyl-*sn*-glycero-3-phospho-1′-glycerol, but the actual combinations must be determined by methods discussed later in this chapter.

The $C_{16}$ and $C_{18}$ fatty acids listed on the first page of this chapter comprise the bulk of the acyl groups found in higher plants, but they are by no means the only ones. Longer chain fatty acids such as arachidonic acid (20:4) are found in algae but are rare in the higher plants with the exception of phosphatidylserine, which contains significant amounts of $C_{20}$ to $C_{26}$ fatty acids.[1450] Shorter chain fatty acids such as lauric acid (12:0) or myristic acid (14:0) are found in significant amounts in mint leaf,[1470] cucurbit seed,[1476] and dill leaf PI,[1470] and in trace amounts in many other plant phospholipids.

## Separation into Molecular Species

Each of the foregoing phospholipid classes comprises a range of individual compounds, the so-called molecular species, which contain fatty acid residues of variable chain lengths and degrees of unsaturation. In the molecular formula given at the beginning of this chapter, the nature of the "Z" group determines the class into which a particular phospholipid falls. In this section, we are concerned with the nature of the "R" groups, $R^1$ and $R^2$, which can be the same or different. Each individual compound in a phospholipid is defined by three variables, $R^1$, $R^2$, and Z.

### *(1) Argentation TLC Method*

Silver ion has a retarding effect on the TLC of unsaturated compounds owing to the formation of a reversible complex between the silver ion and the double bond. This effect has

**Table 4-6** Argentation TLC

| CC | PE (intact)[a] | PC (MADG)[b] | Molecular species |
|---|---|---|---|
| 0 | | | |
| 1 | 0.60 | 0.88 | 16:0/16:1, 16:0/18:1 |
| 2 | 0.48 | 0.76, 0.82 | 16:0/18:2, 18:1/16:1, 18:1/18:1 |
| 3 | 0.30, 0.40 | 0.38, 0.65 | 16:0/18:3, 18:1/18:2 |
| 4 | 0.22 | 0.23 | 18:1/18:3, 18:2/18:2 |
| 5 | 0.12 | | 18:2/18:3 |
| 6 | 0.05 | | 18:3/18:3 |

[a]PE in perilla seed.[2094]

[b]PC in rape cell suspension culture.[2099]

been used to advantage in the separation of intact PC,[2093] PE,[2093,2094] or PG[1566,2095] of plant origin into four to six subclasses of different saturation levels. More often it has been applied to the separation of the 1,2-diacylglycerols (DG) or their acetates (MADG) remaining after removal of the phosphate head group by acetolysis[1845] or by hydrolysis with phospholipase C[2023,2096] followed in some cases by acetylation with acetic anhydride[2097] or acetyl chloride[2098] to prevent isomerization of the DG. Regardless of which variant is used, the fractions separate in order of increasing saturation (Table 4-6). If the subclass comprises DGs or intact PLs, its composition is almost always determined by GC of the fatty acid methyl esters (FAME) after transesterification with methanol/HCl.[2098] If the subclass comprises MADGs, its composition can also be determined by GC[2097] or GC/MS.[1904]

This procedure determines the pairings of the acyl groups in the phospholipids but not their relative positions. For this an additional step is needed, such as selective cleavage of the *sn*-1 acyl group of the DG or MADG with phospholipase $A_2$ followed by a second GC/FAME analysis.[2023] This method has been used in about 20 molecular species determinations (Table 4-6).

### *(2) High-Performance Liquid Chromatography (HPLC) Method*

Reversed-phase HPLC offers a method for separating the phospholipids of each class (PC, PE, etc.) into its individual molecular species, often with baseline resolution, short columns, and isocratic solvents. In general, the retention time increases with increasing chain length and decreases with increasing unsaturation regardless of phospholipid class.[1410,1983] The following procedure is typical:

> *PC, PE, MGDG and DGDG were separated into molecular species on a 3.9 × 300 mm μ Bondapak $C_{18}$ column in MeOH-$H_2O$-MeCN (90.5:7:2.5) at a flow rate of 1.5 ml/min . . . . Phospholipids and galactolipids were solubilized in 0.1 to 0.2 ml of EtOH or MeOH and portions of 10-25 μl (50-150 μg) were applied to the column. After elution, lipids were detected at 205 nm as described above. . . . Lipids from each fraction collected at the exit of HPLC column were extracted according to [Bligh and Dyer[1387]]. For quantification on a mass basis, an appropriate amount of an intl. standard*

*(heptadecanoic acid) was added to the pooled eluate representing each peak. Fatty acid methyl esters from each lipid then were prepared by* trans-*methylation … and analyzed by GC ….*

Demandre, C.; Tremolieres, A.; Justin, A.-M.; Mazliak, P., "Analysis of Molecular Species of Plant Polar Lipids by High Performance and Gas Liquid Chromatography", *Phytochemistry* **1985**, *24*(3), 481–485,[1410] reprinted by permission of Elsevier, © 1985.

Resolution is improved considerably if an ion-pairing reagent such as tetrabutylammonium phosphate is added to the mobile phase; this procedure is applicable to PC and PE,[2100] PI,[2101] PG and DPG,[2102] and PA.[2103] Direct quantitation of the molecular species is possible if the UV detector is replaced by a flame ionization detector (FID)[2104,2105] or by thermospray MS.[2106] An RI detector was used in the original paper on this method.[2107] Derivatization of the phospholipid prior to HPLC, for example by esterification of the P-OH group of PA[2108] or PG[2109] with methanol or of the C-$NH_2$ group of PE or PS with 2,4,6-trinitrobenzenesulfonic acid[2110] is possible but unnecessary.

*(3) Gas-Liquid Chromatography (GLC) Method*

This method, introduced in 1982,[2111] offers an alternative to HPLC and argentation TLC for separating and quantitating plant phospholipids (PC, PE, etc.) into their individual molecular species. Prior to separation, the phosphate group must be removed by hydrolysis with phospholipase C and the resulting diacylglycerol (DG) converted to its acetyl (MADG),[2112] trimethylsilyl (TMSDG)[2111] or *t*-butyldimethylsilyl (tBDMSDG)[2113] derivative. GLC chromatography on a capillary column separates the DG derivatives by carbon number, degree of unsaturation. or both, depending on whether the liquid phase is polar or nonpolar. For example, chromatography of TMS-DG from soybean PI on a 10-m capillary column coated with a polar liquid phase (Supelco SP-2330) at 250 °C gave 13 well-resolved peaks ranging from 16:0/16:0 to 18:2/18:3, whereas an 8-m fused capillary silica column coated with a nonpolar liquid phase (Hewlett-Packard SE-54) at temperatures programmed from 40 to 340 °C gave just two major peaks in the $C_{32}$ to $C_{42}$ range corresponding to various pairings of $C_{16}/C_{18}$ and $C_{18}/C_{18}$ acyl groups, where $C_{16}$ = palmitic acid and $C_{18}$ = stearic, oleic, vaccenic, linoleic or linolenic acid.[2114]

The molecular species are identified in most cases by comparison with the retention times of standards or with the relative retention time factors published by Myher and Kuksis,[2111] confirmed in some cases by GC/MS.[2112,2115] This method, like the first two, does not distinguish isomeric pairs such as 16:0/18:2 and 18:2/16:0. The relative positions of the acyl groups must be determined independently, for example by hydrolysis with phospholipase $A_2$ and GC(FAME) analysis of the fragments. The GLC method has been used in about 20 molecular species determinantions (Table 4-8).

*(4) Mass Spectrometry (MS) Method*

Conventional electron impact (EI) ionization techniques are unsuitable for the present purpose, but the development of "soft" ionization modes such as field desorption (FD),

fast atom bombardment (FAB), or chemical ionization (CI) has enabled MS techniques to be applied to intact phospholipids such as PC, PE, PG, or PI. FD-MS of commercial soybean PC or PE gives molecular species profiles that agree with those of the HPLC or GLC methods. The formation of $[M+Na]^+$ ions can be suppressed by the addition of *p*-toluenesulfonic acid[2122] or enhanced by the addition of NaCl.[2134]

FAB-MS in either the positive or negative mode gives the $[M+H]^+$ or $[M-H]^-$ molecular ions of PC, PE, or PI, but the elevated background levels and increased level of surface reactions make it unsuitable for quantitative measurement.[2134] The background level can be reduced by a special technique that deposits most of the phospholipid on a matrix surface.[2135] Combination of negative-ion FAB-MS with collisional activation of daughter ions (CAD), which requires a triple sector mass spectrometer such as VG ZAB-3F or Kratos MS-50, provides much more complete compositional information. Over 95% of the molecular species reported by GLC for soybean PI were identified and characterized unambiguously by FAB-MS-MS, including low-level isomeric pairs such as 18:0/18:3 and 18:1/18:2. However, this method is also unsuitable for quantitative analysis.[1369,2136]

Isobutane CI-MS has been used to identify the molecular species of soybean PC, PE, and PI[2123,2137] and black mangrove PG.[2138] The $[MH]^+$ peaks are weak or nonexistent, but a method was developed for absolute quantitation based on the diglyceride ion $DG^+$ and internal standards. If two molecular species have the same molecular weight, they can be distinguished by tandem MS-MS daughter analysis.[2123] Other MS methods that have been applied to soybean PI are secondary ion mass spectrometry (SIMS)[2139] and $^{252}Cf$ plasma desorption mass spectrometry (PD-MS).[2140] In one instance, the MS method was applied to spinach PC or PG after removal of the phosphate group by hydrolysis with phospholipase C and conversion to the acetyl derivative MADG.[2141] In all, MS methods have been used in about 12 molecular species determinations (Table 4-8).

### *(5) Random Distribution (1R,2R) Method*

If the acyl group distributions at the *sn*-1 and *sn*-2 positions of a phospholipid are known, the molecular species pairings can be calculated by the 1-random-2-random method, which assumes that each pairing is determined solely by the relative abundance of its partners. The validity of this assumption can be tested by comparing the calculated values with those found experimentally by any of the foregoing methods. Some authors[1845,2023,2094,2114] have reported good agreement while others[2096] have not.

The procedure is best illustrated by a concrete example (Table 4-7, taken from Myher and Kuksis[2114]). Analysis of a purified commercial soybean PI by the GLC/FAME method together with selective hydrolysis of the PI with phospholipase C and independently with phospholipase $A_2$ provide the data shown in Table 4-7, columns 2 and 3. The data shown in columns 4-7 were calculated from various pairings of those of columns 2 and 3 by using the expression mol% DG = mol% (*sn*-1)(*sn*-2)/100; for example, mol% 16:0:18:2 = (67.4)(75.2)/100 = 50.7.

The data in parentheses represent the corresponding values obtained experimentally by the GLC/TMS method.

**Table 4-7** Molecular Species in Soybean PI

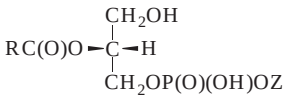
| Fatty acid | Position | | 1-random-2-random distribution[a] | | | |
|---|---|---|---|---|---|---|
| | *sn*-1 | *sn*-2 | 16:0 | 18:1 | 18:2 | 18:3 |
| 16:0 | 67.4 | 5.9 | 4.0 (0.1) | 4.8 (4.3) | 50.7 (57.3) | 5.9 (6.8) |
| 18:0 | 15.8 | 2.1 | 0.9 | 1.1 (1.0) | 11.9 (13.1) | 1.4 (1.3) |
| 18:1 | 3.7 | 7.1 | 0.2 | 0.3 | 2.8 (3.6) | 0.3 |
| 18:2 | 7.7 | 75.2 | 0.4 | 0.5 | 5.8 (6.5)[b] | 0.7 (1.0) |
| 18.3 | 0.8 | 8.7 | 0.05 | 0.06 | 0.6 | 0.07 |

[a]Experimental data in parentheses. Data include reverse isomers.

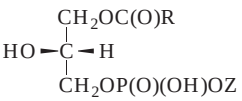
[b]Including 18:1/18:3 and 18:3/18:1, indistinguishable by this method from 18:2/18:2.

# Lysophospholipids

The terms *lysolecithin* (LPC) and *lysocephalin* (LPE) were coined by Levene and Rolf[2142] in 1923 to describe the products obtained by the action of cobra venom on egg yolk PC and PE, respectively. This group now comprises the lysophospholipids LPC, LPE, LPG, LPI, LPS, and LPA and the lysophospholipid derivatives LPIP and NALPE. Each of these compounds can occur in one of two forms, depending on which acyl group is removed from the parent phospholipid. If the terminal acyl group is split off, the product is a 1-lysophospholipid, but if the middle acyl group is split off, the product is a 2-lysophospholipid:




1-LPL




2-LPL

## Occurrence

The first lysophospholipid reported to occur in plants was lysophosphatidylcholine (LPC), isolated from polished rice by Iwata in 1930. The compound, a strong hemolytic agent, formed colorless needles, mp 262-264 °C dec., $[\alpha]_D^{20}$ −4.52° ($CHCl_3$), that yielded palmitic acid, choline, and glycerophosphoric acid upon acid hydrolysis.[1378] LPC was soon shown to be widely distributed among plant seeds,[2143] but the other LPLs were not reported until much later—NALPE (1965) in wheat flour,[1358] LPE and LPS (1967) in wheat starch,[2077] LPI (1971) in several cereal starches,[1499] and LPG (1979) in corn starch.[2074] The occurrence of LPLs in cereal seeds is now well documented,[2144] but their occurrence in leaves, stems, or roots (listed in Table 4-8) remains questionable. Plant cells contain the enzymes phospholipase $A_1$ and $A_2$, which, if not inactivated, can degrade any of the phospholipids to 1-lyso- and 2-lysophospholipids, respectively, during extraction and isolation. These enzymes can be inactivated by steaming or by

| LPL | ZOH component | $RCO_2H$ component | |
|---|---|---|---|
| LPA | H | 16:0 | Palmitic acid |
| LPC | Choline | 18:0 | Stearic acid |
| LPE | Ethanolamine | 18:1 | Oleic acid |
| LPG | Glycerol | 18:2 | Linoleic acid |
| LPS | L-Serine | 18:3 | Linolenic acid |
| LPI | *myo*-Inositol | | |
| LPIP | *myo*-Inositol 4-phosphate | and other long-chain fatty acids | |
| NALPE | *N*-Acylethanolamine | | |

extraction with hot 2-propanol, but in some cases, as for example leaf plasma membrane preparations, which require fractionation prior to extraction, some phospholipid degradation is inevitable.

## Physical Properties

Physical properties have been reported for a few lysophospholipids derived from plant sources without regard to the presence therein of acyl groups of different chain lengths or degrees of unsaturation. Some of these are reported in Table 4-1.

## Extraction

The lysophospholipids are incompletely extracted by the solvents usually employed to extract phospholipids, such as chloroform/methanol, but are efficiently extracted by water-saturated *n*-butanol (WSB) at 90-100 °C. There is no perceptible lipid degradation if the reaction is carried out under nitrogen, and care is taken to inactivate the phospholipases.[1393] The preferred procedure for plant tissues such as wheat starch, which is rich in lysophospholipids, is to remove the PLs by extraction with WSB or other solvent mixture for 10 min at 20 °C, followed by a 3-h extraction at 90-100 °C to remove the LPLs.[1392]

## Separation and Analysis

### *(1) Thin-Layer Chromatography (TLC) Method*

The method of Colborne and Laidman[1393] described on p 155 separates both Pls and LPLs in a single run. The lysophospholipids have much lower $R_f$ values than the phospholipids in both dimensions (Table 4-2).

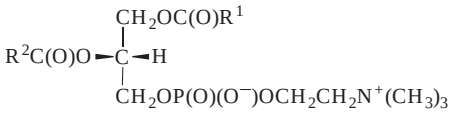
### *(2) High-Performance Liquid Chromatography (HPLC) Method*

The separation of wheat LPLs on a 7μ Lichrosorb Si-60 column, hexane/THF/2-propanol/water mobile phase, and ELS detection gives, in order of elution, NALPE > LPE > LPC for the nonstarch lipids and LPE > LPG > LPC for the starch lipids.[1417] LPC, LPI, and LPS can

be separated on an aminopropyl silica column with ethanol/acetonitrile/10m*M* ammonium phosphate buffer as the mobile phase.[1416]

# PHOSPHATIDYLCHOLINES

This group comprises the phosphatidylcholines (PC) and the lysophosphatidylcholines (LPC).



PC, $R^1 = R^2 =$ alkyl
1-LPC, $R^1 = H$, $R^2 =$ alkyl
2-LPC, $R^1 =$ alkyl, $R^2 = H$

## Phosphatidylcholines

### Physical Properties

1,2-Dipalmitoyl-*sn*-glycero-3-phosphocholine (DPPC), 16:0/16:0 PC, $C_{40}H_{80}NO_8P$. *(R)-4-Hydroxy-N,N,N-trimethyl-10-oxo-7-[(1-oxohexadecyl)oxy]-3,5,9-trioxa-4-phosphapentacosan-1-aminium Hydroxide, inner salt, 4-Oxide.*

DPPC [R.N. 63-89-8]: Plates, X-ray[2145]; electron diffraction,[2146] ORD and CD (figs.)[2147]; conformation.[2148] Spectra: IR,[2149] Raman (fig.).[2150] EI-MS (fig.),[2151] FAB-MS (fig.),[2152] FD-MS (fig.),[2122] CIMS,[2153] SIMS (fig.),[2152] LSIMS,[2154] FAB MS/MS,[2155] and MALDI FT-ICR-MS.[1370] Chromatography: SFC.[2156] The anhydrous salt is over 10 times more soluble than its hydrate in solvents such as benzene.[2145] *Hydrate* [R.N. 60422-19-7]: Crystals, mp 235-236 °C, $[\alpha]_D^{25}$ +7.0° ($CHCl_3$),[2157] soluble in chloroform and hot dioxane, very slightly soluble in other solvents[2158]; countercurrent distribution[2159]; fluorescence polarization[1631]; DSC.[2160] Spectra: IR (fig.),[2161] FTIR,[2162] $^1H$ and $^{13}C$ NMR (figs.),[118] $^{31}P$ NMR (fig.),[2163] $^{14}N$ NMR (fig.),[2164] X-ray (photo.),[2158] PES.[1381] Chromatography: PC,[2165] TLC,[2166] HPTLC,[1405] HPLC.[2107] *Dihydrate* [R.N. 68573-30-8]: Orthorhombic crystals, X-ray,[2167] DTA.[2167] Spectra: Raman,[2168] $^{13}C$ and $^{31}P$ CP-MAS NMR (figs.).[2169]
$[CdCl_2]_3[DPPC{\cdot}H_2O]_2$: Amorphous solid.[2158]

1-Palmitoyl-2-oleoyl-*sn*-glycero-3-phosphocholine (POPC), 16:0/18:1 PC, $C_{42}H_{82}NO_8P$. *[R-(Z)]-4-Hydroxy-N,N,N-trimethyl-9-oxo-7-[[(1-oxohexadecyl)oxy]methyl]-3,5,8-trioxa-4-phosphahexacos-17-en-1-aminium Hydroxide, inner salt, 4-Oxide.*

POPC [R.N.26853-31-6]: $[\alpha]_D^{25}$ +6.3° ($CHCl_3$/MeOH),[2170] CD.[2147] Spectra: FTIR,[2171] Raman,[2172] $^1H$ and $^{13}C$ NMR (figs.),[2173] 2d-[$^1H$][$^{13}C$] NMR (fig.),[2174] EI-MS (fig.),[2175] CI-MS (fig.), [2153] FAB-MS (fig.),[2176] FD-MS,[2177] PD-MS (fig.),[2140] MALDI-MS (fig.),[2178] LSI-MS (fig.),[2139] FAB-MS/MS (fig.),[2176] MALDI FT-ICR MS/MS (fig.),[1370] CID-MS/MS.[2179] Chromatography: Silicic acid column,[2170] HPLC,[2107] HPLC-CIMS.[2180] Electrophoresis: CE (fig.).[2181] *Hemihydrate*: mp 225-230 °C, $[\alpha]_D^{20}$ −7.57° [*sic*] ($CHCl_3$/MeOH),[2182] DSC.[2183] Spectra: ESR.[2184] Chromatography: TLC,[2166] silica gel column.[2182]

1-Palmitoyl-2-linoleoyl-*sn*-glycero-3-phosphocholine (PLPC), 16:0/18:2 PC, $C_{42}H_{80}NO_8P$. *[R-(Z,Z)]-4-Hydroxy-N,N,N-trimethyl-9-oxo-7-[[(1-oxohexadecyl)oxy]methyl]-3,5,8-trioxa-4-phosphahexacosa-17,20-dien-1-aminium Hydroxide, inner salt, 4-Oxide.*

PLPC [R.N. 17708-90-6; see also 6931-84-6]: Pale yellow oil.[1788] Spectra: $^{13}C$ and $^{31}P$ NMR,[2083] EI-MS,[2185] FD-MS,[2177] FAB-MS and FAB-MS/MS,[2176] SIMS,[2139] CID-MS-MS.[2179] Chromatography: HPLC.[2107]

1-Palmitoyl-2-linolenoyl-*sn*-glycero-3-phosphocholine (PLnPC), 16:0/18:3 PC, $C_{42}H_{78}NO_8P$. *[R-(Z,Z,Z)]-4-Hydroxy-N,N,N-trimethyl-9-oxo-7-[[(1-oxohexadecyl)oxy]methyl]-3,5,8-trioxa-4-phosphahexacosa-17,20,23-trien-1-aminium Hydroxide, inner salt, 4-Oxide.*

PLnPC [R.N. 35418-56-5 or 95268-94-3]: $[\alpha]_D^{20}$ −2.9° ($CHCl_3$).[2186] Spectra: $^1H$ and $^{31}P$ NMR.[2186] Chromatography: Ag-TLC,[2099] HPLC.[2100]

1-Stearoyl-2-oleoyl-*sn*-glycero-3-phosphocholine (SOPC), 18:0/18:1 PC, $C_{44}H_{86}NO_8P$. *[R-(Z)]-4-Hydroxy-N,N,N-trimethyl-10-oxo-7-[(1-oxo-9-octadecenyl)oxy]-3,5,9-trioxa-4-phosphaheptacosan-1-aminium Hydroxide, inner salt, 4-Oxide.*

SOPC [R.N. 56421-10-4]: EI-MS (fig.),[2151] FD-MS,[2122] FAB-MS and FAB-MS/MS,[2176] CID-MS-MS.[2179] Chromatography: LC-MS (fig.).[2187] *Monohydrate*: White solid, mp 230-231 °C, $[\alpha]_D^{20}$ +6.0° ($CHCl_3$), soluble in $CHCl_3$, methanol, ethanol, and ether, fairly soluble in acetone, insoluble in water[2188]; countercurrent distribution[2159]; DTA[2189]; DSC[2190]; monolayer film properties.[2191] Spectra: IR (fig.),[2188] $^{13}C$ NMR.[2192] Chromatography: PC, TLC, silicic acid column,[2188] HPLC.[2107]
$[CdCl_2]_3[SOPC{\cdot}H_2O]_2$: Solid.[2188]

1-Stearoyl-2-linoleoyl-*sn*-glycero-3-phosphocholine (SLPC), 18:0/18:2 PC, $C_{44}H_{84}NO_8P$. *[R-(Z,Z)]-4-Hydroxy-N,N,N-trimethyl-10-oxo-7-[(1-oxo-9,12-octadecadienyl)oxy]-3,5,9-trioxa-4-phosphaheptacosan-1-aminium Hydroxide, inner salt, 4-Oxide.*

SLPC [R.N. 27098-24-4]: Spectra: FD-MS,[2122] LIMS (fig.),[2154] CID-MS-MS.[2179] Chromatography: HPLC.[2100] *Hydrate*: mp 163.0-165.0 °C, $[\alpha]_D^{20}$ +5.02° ($CHCl_3$),[2193] monolayer film properties,[2191] DSC.[2194] Spectra: UV,[2194] IR (fig.),[2193] $^{13}C$ NMR (fig.).[2195] Chromatography: PC,[2193] TLC,[2196] silicic acid column.[2195]

1-Stearoyl-2-linolenoyl-*sn*-glycero-3-phosphocholine (SLnPC), 18:0/18:3 PC, $C_{44}H_{82}NO_8P$. *[R-(Z,Z,Z)]-4-Hydroxy-N,N,N-trimethyl-10-oxo-7-[(1-oxo-9,12,15-octadecatrienyl)oxy]-3,5,9-trioxa-4-phosphaheptacosan-1-aminium Hydroxide, inner salt, 4-Oxide.*

SLnPC [R.N. 35418-57-6; see also 40811-59-4]: $[\alpha]_D^{20}$ −6.4° ($CHCl_3$).[2186] Spectra: $^1H$ and $^{31}P$ NMR.[2186] Chromatography: HPLC.[2051] *Hydrate*: Monolayer film properties,[2191] DSC.[2194] Spectra: UV.[2194] Chromatography: TLC, silicic acid column.[2194]

1,2-Dioleoyl-*sn*-glycero-3-phosphocholine (DOPC), 18:1/18:1 PC, $C_{44}H_{84}NO_8P$. *[R-(Z,Z)]-4-Hydroxy-N,N,N-trimethyl-10-oxo-7-[(1-oxo-9-octadecenyl)oxy]-3,5,9-trioxa-4-phosphaheptacos-18-en-1-aminium Hydroxide, inner salt, 4-Oxide.*

DOPC [R.N. 4235-95-4; see also 10015-85-7]: Colorless waxlike substance, soluble in chloroform and ethanol, less soluble in acetone, insoluble in ether, water[2197]; $[\alpha]_D^{22}$ +5.4° (1:1 $CHCl_3$/MeOH),[2197] countercurrent distribution.[2159] CD (fig.).[2147] Spectra: IR (fig.),[2198] Raman (fig.).[2199] PES,[1381] EI-MS (fig.),[2151] FAB-MS,[2200] FD-MS,[2177] CIMS,[2153]

LSIMS (fig.).[2154] Chromatography: PC,[2197] HPTLC,[1405] HPLC,[2107] silicic acid column,[2197] silica gel column.[2201] *Hydrate*: Waxlike substance, readily soluble in chloroform, methanol, ethanol, ether, and 90% acetone, moderately soluble in warm petroleum ether[2202]; $[\alpha]_D^{25}$ +6.2° (1:1 $CHCl_3$/MeOH),[2202] monolayer film properties,[2191] DSC.[2190] Spectra: IR (fig.), [2202] $^1$H NMR (fig.),[2203] $^{13}$C NMR,[2083] $^{31}$P NMR (fig.),[2163] $^{14}$N NMR.[2204] Chromatography: TLC,[2166] silicic acid column.[2202]
$[CdCl_2]_3$[DOPC.$H_2O$]$_2$: Solid,[2197] $[\alpha]_D$ +3.7° ($CHCl_3$).[2202]

1-Oleoyl-2-linoleoyl-*sn*-glycero-3-phosphocholine (OLPC), 18:1/18:2 PC, $C_{44}H_{82}NO_8P$. *[R-(Z,Z,Z)]-4-Hydroxy-N,N,N-trimethyl-10-oxo-7-[(1-oxo-9,12-octadecadienyl)oxy]-3,5,9-trioxa-4-phosphaheptacos-18-en-1-aminium Hydroxide, inner salt, 4-Oxide.*
OLPC [R.N. 17041-44-0; see also 99166-28-6]: FD-MS,[2122] HPLC.[2100]

1-Oleoyl-2-linolenoyl-*sn*-glycero-3-phosphocholine (OLnPC), 18:1/18:3 PC, $C_{44}H_{80}NO_8P$. *[R-(all Z)]-4-Hydroxy-N,N,N-trimethyl-10-oxo-7-[(1-oxo-9,12,15-octadecatrienyl)oxy]-3,5,9-trioxa-4-phosphaheptacos-18-en-1-aminium Hydroxide, inner salt, 4-Oxide.*
OLnPC [R.N. 105017-24-1; see also 74936-57-5, 96497-78-8, 120502-93-4]: HPLC.[2105]

1,2-Dilinoleoyl-*sn*-glycero-3-phosphocholine (DLPC), 18:2/18:2 PC, $C_{44}H_{80}NO_8P$. *[R-(all Z)]-4-Hydroxy-N,N,N-trimethyl-10-oxo-7-[(1-oxo-9,12-octadecadienyl)oxy]-3,5,9-trioxa-4-phosphaheptacosa-18,21-dien-1-aminium Hydroxide, inner salt, 4-Oxide.*
DLPC [R.N. 998-06-1; see also 6542-05-8, 81902-03-3]: Glass,[2201] solubility in $CHCl_3$ 0.8 mol/L at 20 °C.[2205] Spectra: IR (fig.),[2205] FD-MS (fig.),[2177] CIMS,[2153] LIMS.[2154] Chromatography: Silica gel column.[2201] *Hydrate*: $[\alpha]_D^{25}$ +6.02° ($CHCl_3$),[2206] DSC.[2207] Spectra: UV, [2207] IR (fig.),[2206] $^1$H NMR,[2208] $^{13}$C and $^{31}$P NMR.[2083] Chromatography: PC,[2206] TLC,[2166] silicic acid column,[2206] HPTLC.[1405]

1-Linoleoyl-2-linolenoyl-*sn*-glycero-3-phosphocholine (LLnPC), 18:2/18:3 PC, $C_{44}H_{78}NO_8P$. *[R-(all Z)]-4-Hydroxy-N,N,N-trimethyl-10-oxo-7-[(1-oxo-9,12,15-octadecatrienyl)oxy]-3,5,9-trioxa-4-phosphaheptacosa-18,21-dien-1-aminium Hydroxide, inner salt, 4-Oxide.*
LLnPC [R.N. 85046-19-1; see also 105120-83-0]: FD-MS,[2122] CIMS,[2153] HPLC.[2100]

1,2-Dilinolenoyl-*sn*-glycero-3-phosphocholine (DLnPC), 18:3/18:3 PC, $C_{44}H_{76}NO_8P$. *[R-(all Z)]-4-Hydroxy-N,N,N-trimethyl-10-oxo-7-[(1-oxo-9,12,15-octadecatrienyl)oxy]-3,5,9-trioxa-4-phosphaheptacosa-18,21,24-trien-1-aminium Hydroxide, inner salt, 4-Oxide.*
DLnPC [R.N. 2701-19-1; see also 40811-59-4]: DSC.[2207] Spectra: UV,[2209] $^1$H NMR (fig.),[2209] FD-MS,[2177] CIMS.[2153] Chromatography: TLC,[2209] HPTLC,[1405] HPLC.[2100]

## Molecular Species Composition

The molecular species composition of phosphatidylcholine in plants, determined by any of the methods described on pages 168–171, is given in Table 4-8.

## Synthesis

DPPC may be prepared (a) by phosphorylation of 1,2-dipalmitoyl-*sn*-glycerol with phenyl phosphorodichloridate,[2158] methyl *N,N*-diisopropylaminophosphorochloridite,[2210] or

$PCl_3$/imidazole[2211] followed by choline chloride or choline tosylate, (b) by base-catalyzed acylation of *sn*-glycero-3-phosphocholine or its $CdCl_2$ complex with palmitoyl chloride,[2212] palmitic anhydride,[2198] or *N*-palmitoylimidazole,[2213] or (c) by stepwise reaction of 1,2-dipalmitoyl-*sn*-glycerol with 2-bromoethyl phosphorodichloridate[2214] or 2-chloro-2-oxo-1,3,2-dioxaphospholane[2215] and trimethylamine. POPC may be prepared (a) by acylation of 1-palmitoyl-*sn*-glycero-3-phosphocholine with oleoyl chloride[2170] or oleic anhydride,[2173] or with 2-thiopyridyl oleate in the presence of silver perchlorate,[2216] (b) by acylation of 1-*O*-trityl-2-oleoyl-*sn*-glycero-3-phosphocholine with palmitic anhydride or *N*-palmitoyltriazolide,[2182] or (c) by reaction of the methyl ester of 1-palmitoyl-2-oleoyl-*sn*-glycero-3-phosphoethylene bromohydrin with trimethylamine.[2217] PLPC may be prepared by acylation of 1-palmitoyl-*sn*-glycero-3-phosphocholine with linoleic acid in the presence of *N*,*N*′-carbonyldiimidazole[289] or with 2-thiopyridyl linoleate in the presence of silver perchlorate.[2216] PLnPC may be prepared by acylation of 1-palmitoyl-*sn*-glycero-3-phosphocholine with linolenic anhydride[2186] or of its $CdCl_2$ complex with linolenoyl chloride.[2218]

SOPC may be prepared by the reaction of silver benzyl 1-stearoyl-2-oleoyl-*sn*-glycero-phosphate with 2-bromoethyltrimethylammonium picrate.[2188] SLPC may be prepared (a) by phosphorylation of 1-stearoyl-2-linoleoyl-*sn*-glycerol with $POCl_3$ and choline chloride,[2193] (b) by condensation of 1-stearoyl-2-linoleoyl-*sn*-glycerol 3-iodohydrin with silver 2-chloroethyl *p*-nitrobenzyl phosphate,[2196] or (c) by acylation of 1-stearoyl-*sn*-glycero-3-phosphocholine (SHPC) with linoleic anhydride.[2194] SLnPC may be prepared by acylation of 1-stearoyl-*sn*-glycero-3-phosphocholine with linolenic anhydride[2186] or of its $CdCl_2$ complex with linolenoyl chloride[2218] or linolenic anhydride.[2194]

DOPC may be prepared (a) by acylation of *sn*-glycero-3-phosphocholine with oleoyl chloride in the presence of $CdCl_2$,[2219] with oleic anhydride in the presence of tetraethylammonium oleate,[2220] sodium oleate,[2198] or 4-pyrrolidinopyridine,[2221] or with oleic imidazolide in the presence[2209] or absence[2201] of a strong base, (b) by phosphorylation of 1,2-dioleoyl-*sn*-glycerol with $POCl_3$ and choline chloride (or iodide),[2222] or with 2-chloro-2-oxo-1,3,2-dioxaphospholane and trimethylamine,[2223] or (c) by the reaction of 1,2-dioleoyl-*sn*-glycerol-3-ethylenechlorohydrin with trimethylamine.[2202] OLPC may be prepared by stepwise acylation of the barium salt of *sn*-glycero-3-phosphoethylene chlorohydrin with oleoyl chloride and linoleoyl chloride followed by reaction with trimethylamine.[2224]

DLPC may be prepared (a) by acylation of *sn*-glycero-3-phosphocholine or its $CdCl_2$ complex with linoleoyl chloride in the presence of 4-pyrrolidinopyridine[2221] or potassium linoleate,[2225] or with *N*-linoleoylimidazole in the presence[2209] or absence[2201] of a strong base, (b) by phosphorylation of 1,2-dilinoleoyl *sn*-glycerol with $POCl_3$ and choline chloride,[2193] (c) by the reaction of 1,2-dilinoleoyl-*sn*-glycero-3-phosphoethylene chlorohydrin with trimethylamine,[2224] or (d) by condensation of 1-linoleoyl-*sn*-glycero-3-phosphocholine (LHPC) with linoleic acid in the presence of DCC.[2208] DLnPC may be prepared by acylation of *sn*-glycero-3-phosphocholine or its $CdCl_2$ complex with linolenic anhydride[2226] or *N*-linolenoylimidazole.[2209,2227]

**Table 4-8** Molecular Species Composition: Phosphatidylcholines (mol%)

| No. | Plant part | Method | 16:0 16:0 | 16:0 18:1 | 16:0 18:2 | 16:0 18:3 | 18:0 18:1 | 18:0 18:2 | 18:0 18:3 | 18:1 18:1 | 18:1 18:2 | 18:1 18:3 | 18:2 18:2 | 18:2 18:3 | 18:3 18:3 | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Arabidopsis thaliana* (L.) Heynh (Mouse-Ear Cress) | | | | | | | | | | | | | | | | |
| 1 | Leaf plasma membrane | GLC | 0.4[a] | 2.9 | 32.1 | 23.6 | 0.6 | 0.4 | 0.8 | 2.3 | 2.7 | 14.8[b] | | 13.1 | 4.0 | 1478 |
| *Arachis hypogaea* L. (Peanut) | | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | | | | | | | | | 59.3 | | 40.7 | | | 2116 |
| *Avena sativa* L. (Oats) | | | | | | | | | | | | | | | | |
| 1 | Leaf plasma membrane | GLC | 1.8[a] | 5.6 | 34.3 | 19.9 | 0.7 | | 0.4 | 0.8 | 4.4 | 14.9[b] | | 9.6 | 3.7 | 1502 |
| 1 | Root plasma membrane | GLC | | | 55 | 14 | | | | | | | 23 | 8 | | 2113 |
| *Brassica napus* L. (Rape) | | | | | | | | | | | | | | | | |
| 1 | Cell susp. culture | AgTLC | | 19[c] | 8 | 29 | | | | 16[d] | 10 | 18 | | | | 2099 |
| *Brassica napus* L. (Rape, low erucic acid (Canola)) | | | | | | | | | | | | | | | | |
| 1 | Leaf | HPLC | | 1.8 | 11.5 | 17.9 | | | 3.9 | | 4.0 | | 10.1 | 26.1 | 24.6 | 2117 |
| *Brassica oleracea* L. ssp. *botrytis* L. (Cauliflower) | | | | | | | | | | | | | | | | |
| 1 | Inflorescence | AgTLC | | 1.2 | 7.5 | 37.2 | | | | 0.4 | 3.3 | 18.6 | | 6.8 | 21.6 | 2096 |
| *Camellia sinensis* L. (Tea) | | | | | | | | | | | | | | | | |
| 1 | Pollen | HPLC | | | | 60 | | | | | | | | | 25 | 1558 |
| *Carthamus tinctorius* L. (Safflower) | | | | | | | | | | | | | | | | |
| 1 | Seed | AgTLC | 0.5 | 4.2 | 34.7 | | (18:2/18:1, 5.0) | | | 1.4 | 8.0 | | 44.8 | | | 2118 |
| *Crambe amabilis* Butkov and Majlin | | | | | | | | | | | | | | | | |
| 1 | Seed | 1R,2R | 0.5 | 5.5 | 4.9 | 3.4 | 1.0 | 1.0 | | 12.6 | 12.9 | 7.5 | 7.5 | 5.3 | 7.2 | 2119 |
| *Daucus carota* L. (Carrot) | | | | | | | | | | | | | | | | |
| 1 | Cell culture | AgTLC | | 2.2 | 43.3 | | | | | | 11.8 | | 25.1 | 17.6 | | 1648 |
| *Dianthus caryophyllus* L. (Carnation) | | | | | | | | | | | | | | | | |
| 1 | Flower microsomal membr. | GLC | | 2.5 | 50.7 | 2.1 | | 0.8 | (16:0/18:0, 0.5) | | 4.4 | 1.4 | 34.0 | 2.9 | | 1652 |
| *Diptychocarpus strictus* (Fisch.) Trautv. | | | | | | | | | | | | | | | | |
| 1 | Seed | 1R,2R | 0.3 | 5 | 6.1 | 9 | 1 | 1.2 | 1.7 | 7.5 | 8.3 | 13.2 | 5 | 8.1 | 9 | 959 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Echium plantagineum* L. (Salvation Jane) | | | | | | | | | | | | | | | |
| 1 | Leaf | AgTLC | | | 18 | 10 | | | | 5[e] | 6.5[e] | 5 | 14[e] | 2.5 | 2120 |
| *Glycine max* (L.) Merr. (Soybean) | | | | | | | | | | | | | | | |
| 1 | Seed | $Br_2$ | | | 19.1 | | | | 4.7 | 63.0 | | 13.5 | | | 2121 |
| 1 | Seed | AgTLC | | 3.1 | 24.0 | | (18:3/18:2, 6.9) | 3.5 | 1.8 | 8.9 | | 39.7 | 1.8 | | 2118 |
| 1 | Seed | GLC | | 2.6 | 25.3 | 2.4 | 0.5 | 6.6 | 0.4 | 0.7 | 8.0 | | 42.4 | 8.3 | 0.5 | 2111 |
| 1 | Seed | FD-MS | 1.0 | 6.0 | 26.7 | | 1.6 | | | 8.9[f] | 13.8 | | 34.0 | 6.9 | | 2122 |
| 1 | Seed | CI-MS | | 2.7 | 25.7 | 2.5 | 0.9 | 8.5 | 0.6 | 1.0 | 11.9 | | 38.9 | 6.9 | 0.4 | 2123 |
| 1 | Seed | HPLC | 0.5 | 8.2[f] | 24.8 | 3.3 | 0.6 | | 0.3 | 0.7 | 7.8 | 3.5 | 38.7 | 10.7 | 0.9 | 1693 |
| 1 | –, hypocotyl | AgTLC | | | 24 | 9 | | 8 | | | 7 | | 46 | 2 | Trace | 1690 |
| 1 | –, cotyledon | AgTLC | | | 27 | 1 | | 10 | | | 15 | | 36 | 3 | Trace | 1690 |
| 1 | –, cotyledon | HPLC | | | 19.24 | 32.46 | | | | 9.38 | 7.85 | 3.43 | 4.70 | 4.45 | 10.46 | 2124 |
| 1 | –, axis | HPLC | | | 23.9 | 15.8 | | | | 5.4 | Trace | Trace | 37.5 | 17.4 | Trace | 2124 |
| 1 | Leaf | HPLC | | | 8.75 | 39.27 | | | | 0.91 | 2.23 | 1.96 | 17.21 | 10.58 | 15.44 | 2124 |
| 1 | Stem | HPLC | | | 11.46 | 43.26 | | | | 3.21 | 2.87 | 2.98 | 14.23 | 6.62 | 12.55 | 2124 |
| 1 | Root | HPLC | | | 22.97 | 38.62 | | | | 6.62 | 6.70 | 4.40 | 2.20 | 3.97 | 8.52 | 2124 |
| 1 | Seedling, microsomes | HPLC | 0.4 | 3.2 | 26.8 | 5.9 | 0.4 | 5.4 | 1.0 | 0.5 | 9.2 | 1.2 | 35.1 | 9.9[e] | 0.9 | 2125 |
| *Gossypium barbadense* L. (Sea Island Cotton) | | | | | | | | | | | | | | | | |
| 1 | Seed kernel | 1R,2R | 2.0 | 9.8 | 18.0 | | 0.8 | 1.5 | | 9.2 | 16.2 | | 20.1 | | | 1709 |
| *Gossypium hirsutum* L. (Upland Cotton) | | | | | | | | | | | | | | | | |
| 1 | Seed | 1R,2R | 3.1 | 14.3 | 22.8 | | 1.2 | 1.4 | | 5.6 | 12.7 | | 23.7 | | | 2098 |
| *Helianthus annuus* L. (Sunflower) | | | | | | | | | | | | | | | | |
| 1 | Seed | 1R,2R | 0.4 | 3.5 | 14.4 | | 1.7 | 7.0 | | 2.3 | 9.3 | | 44.6 | | | 2126 |
| *Hibiscus cannabinus* L (Kenaf) | | | | | | | | | | | | | | | | |
| 1 | Seed | 1R,2R | 1.2 | 12.5 | 19.2 | 0.7 | 0.8 | 1.2 | | 10.3 | 16.4 | 0.6 | 16.9 | 0.6 | | 1377 |
| *Hordeum vulgare* L. (Barley) | | | | | | | | | | | | | | | | |
| 1 | Leaf | HPLC | | | 25.2 | 46.1[b] | | | | | | | | 21.5 | 7.1 | 2127 |

[a]Including 14:0/18:0; [b]Including 18:2/18:2 (LL); [c]Including 16:0/16:1; [d]Including 18:1/16:1 PG; [e]*sn*-1/*sn*-2 positions reversed; [f]Including 18:0/18:2 (SL); [g]Including 18:3/18:2 (LnL); [h]Including 18:0/18:3 (SLn).

*Continued*

**Table 4-8** Molecular Species Composition: Phosphatidylcholines (mol%)—cont'd

| No. | Plant part | Method | 16:0 16:0 | 16:0 18:1 | 16:0 18:2 | 16:0 18:3 | 18:0 18:1 | 18:0 18:2 | 18:0 18:3 | 18:1 18:1 | 18:1 18:2 | 18:1 18:3 | 18:2 18:2 | 18:2 18:3 | 18:3 18:3 | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Lavandula vera* DC (English Lavender) | | | | | | | | | | | | | | | | |
| 1 | Cell culture | AgTLC | | 12.2 | 11.7 | 17.3 | 7.1 | 4.6 | 15.8 | 9.6 | 7.1 | 6.1 | 0.5 | (16:0/18:0, 8.1) | | 1765 |
| *Lilium longiflorum* Thunb. (Trumpet Lily) | | | | | | | | | | | | | | | | |
| 1 | Pollen | HPLC | 1.7 | | 18.5 | 36.0 | | | | | | | 6.5 | 17.6[g] | 11.4 | 1769 |
| *Lycopersicon esculentum* Mill. (Tomato) | | | | | | | | | | | | | | | | |
| 1 | Fruit, pericarp | GLC | 0 | 8.0 | 48.9 | 8.0 | | (16:1/18:2, 13.4) | | | | | 13.6 | 3.9 | 0 | 2128 |
| *Lycoris radiata* Herb. (Red Spiderlily) | | | | | | | | | | | | | | | | |
| 1 | Flower | Prep. TLC | 88.7 | | 11.3 | | | | | | | | | | | 1788 |
| *Malus domestica* Borkh. (Apple) | | | | | | | | | | | | | | | | |
| 1 | Fruit, embryo | HPLC | | 17 | 14 | | | 3 | | 19 | 20 | | 27 | | | 2129 |
| *Medicago media* Pers. (Alfalfa) | | | | | | | | | | | | | | | | |
| 1 | Leaf | AgTLC | | 2.8 | 31.0[f] | 32.7[h] | | | | | | | 6.9 | 13.1 | 10.1 | 2130 |
| *Nicotiana tabacum* L. (Tobacco) | | | | | | | | | | | | | | | | |
| 1 | Leaf | HPLC | | | 17.3 | 42.2 | | | | | | | 8.9 | 17.9 | 14.5 | 1410 |
| 1 | Cell culture | AgTLC | | 11.5 | 48.0 | 15.6 | | | 8.1 | | 3.0 | 3.2 | 8.2 | 2.4 | | 1495 |
| *Oryza sativa* L. (Rice) | | | | | | | | | | | | | | | | |
| 1 | Bran, glutinous | AgTLC | | 26.8 | 14.3 | | (18:2/18:1, 9.3) | | | 29.3 | 12.5 | | 7.8 | | | 1845 |
| 1 | Bran, glutinous | 1R,2R | | 21.3 | 12.8 | | (18:2/18:1, 13.7) | | | 23.6 | 14.2 | | 8.3 | | | 1845 |
| 1 | Bran, nonglutinous | AgTLC | | 18.5 | 20.3 | | (18:2/18:1, 10.1) | | | 19.6 | 18.8 | | 12.7 | | | 1845 |
| 1 | Bran, nonglutinous | 1R,2R | | 16.4 | 18.0 | | (18:2/18:1, 11.9) | | | 15.5 | 17.1 | | 13.1 | | | 1845 |
| *Phaseolus coccineus* L. (Scarlet Runner Bean) | | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | 0.5 | 6.1[f] | 25.2 | 15.3 | <0.1 | | 1.9 | 1.3 | 6.9 | 4.9 | 15.9 | 15.9 | 5.9 | 1693 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Phaseolus vulgaris* L. (Kidney Bean) | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | 1.5 | 11.2[f] | 20.6 | 19.6 | 1.0 | | 1.6 | 3.2 | 9.2 | 8.6 | 6.7 | 11.5 | 5.2 | 1693 |
| *Picea abies* (L.) Karst. (Spruce) | | | | | | | | | | | | | | | |
| 1 | Shoot | GLC | | 11.9 | 26.2 | 1.8 | | 6.6 | | 12.2 | 16.3 | | 19.4 | | | 2115 |
| *Pinus nigra* Arnold (Black Pine) | | | | | | | | | | | | | | | |
| 1 | Needle (leaf) | HPLC | <1 | 1 | 25 | 6 | | 4 | | | 6 | 8 | 15 | 5 | 1 | 1892 |
| *Pisum sativum* L. (Pea) | | | | | | | | | | | | | | | |
| 1 | Seed | AgTLC | | 7.9 | 15.2 | | 4.8 | | | 38.6 | 3.4 | | 30.1 | | | 1904 |
| 1 | Seed | HPLC | 0.1 | 17.0[f] | 14.8 | 1.7 | 4.4 | | 0.5 | 15.8 | 26.4 | 2.1 | 14.7 | 2.3 | 0.2 | 1693 |
| 1 | Leaf | HPLC | | Trace | 28.0 | 16.0 | 1.5 | 1.3 | 2.6 | | 3.2 | 2.2 | 21.2 | 17.8[e] | 6.2 | 2125 |
| *Raphanus sativus* L. (Radish) | | | | | | | | | | | | | | | |
| 1 | Seedling | HPLC | 11.7 | 8.8 | 14.4 | 16.1 | | 8.8 | 3.8 | | 11.2 | 11.1 | 5.8 | 12.0 | 5.1 | 2131 |
| *Rauvolfia serpentina* (L.) Benth. ex Kurz (Indian Snakeroot) | | | | | | | | | | | | | | | |
| 1 | Cell culture | AgTLC | | | 73.7 | 1.6 | Trace | 9.9 | 0.6 | 2.1 | | | | 12.1 | | 1495 |
| *Secale cereale* L. (Rye) | | | | | | | | | | | | | | | |
| 2 | Grain (1) | HPLC | | 7 | 28 | 5 | | | | 3 | 13 | 5 | 30 | 8 | 1 | 1957 |
| | Grain (2) | HPLC | | 5 | 23 | 2 | | | | 2 | 18 | 3 | 38 | 8 | 1 | 1957 |
| 1 | Leaf plasma membrane | GLC | 0.5[a] | 2.4 | 27.4 | 24.9 | 0.3 | | 1.4 | 1.8 | 1.7 | 14.8[b] | | 14.0 | 8.1 | 1502 |
| *Solanum tuberosum* L. (Potato) | | | | | | | | | | | | | | | |
| 1 | Tuber | HPLC | | | 36.3 | 10.4 | | 7.1 | | | | | 32.5 | 13.7 | Trace | 1410 |
| 1 | –, microsomes | HPLC | | 35.5 | 10.1 | | 6.9 | 2.1 | | | | 31.8 | 13.4 | | Trace | 2132 |
| *Spinacia oleracea* L. (Spinach) | | | | | | | | | | | | | | | |
| 1 | Leaf | HPLC | | | 5.4 | 54.1 | (18:3/18:2, 0.9) | | | 3.7 | 5.5 | 2.9 | 16.1 | 7.9 | 3.5 | 2105 |
| 1 | Leaf | HPLC | | 3.6 | 4.7 | 15.5 | | | | 6.9 | 6.5 | 9.0 | 11.6 | 13.8 | 28.3 | 2133 |
| *Triticum aestivum* L. (Wheat) | | | | | | | | | | | | | | | |
| 1 | Germ oil | AgTLC | | 6.9 | 28.4 | (18:3/18:2, 3.6) | | | 1.7 | 2.5 | 11.8 | 0.4 | 36.3 | 2.0 | | 2118 |
| 1 | Flour | AgTLC | | 6.1 | 27.8 | 1.3 | 0.2 | 2.0 | 0.1 | 1.2 | 6.2 | 0.1 | 39.8 | | | 2023 |
| 1 | Flour | 1R,2R | 1.0 | 6.1 | 29.3 | 1.3 | 0.4 | 2.1 | 0.1 | 1.3 | 6.0 | 0.3 | 38.1 | 1.7 | 0.1 | 2023 |
| 1 | Flour | HPLC | | 13.44 | 42.13 | 1.12 | | | | 2.80 | 11.36 | 0.84 | 24.88 | 1.17 | | 2021 |
| *Vicia faba* L. (Broad Bean) | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | 0.2 | 15.8[f] | 16.6 | 0.2 | 3.3 | | 0.5 | 17.0 | 26.8 | 1.3 | 17.4 | 0.9 | 0.1 | 1693 |

[a]Including 14:0/18:0; [b]Including 18:2/18:2 (LL); [c]Including 16:0/16:1; [d]Including 18:1/16:1 PG; [e]*sn*-1/*sn*-2 positions reversed; [f]Including 18:0/18:2 (SL); [g]Including 18:3/18:2 (LnL); [h]Including 18:0/18:3 (SLn).

*Continued*

**Table 4-8** Molecular Species Composition: Phosphatidylcholines (mol%)—cont'd

| No. | Plant part | Method | 16:0 16:0 | 16:0 18:1 | 16:0 18:2 | 16:0 18:3 | 18:0 18:1 | 18:0 18:2 | 18:0 18:3 | 18:1 18:1 | 18:1 18:2 | 18:1 18:3 | 18:2 18:2 | 18:2 18:3 | 18:3 18:3 | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Vigna angularis* (Willd.) Ohwi and Ohashi (Adzuki Bean) | | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | | 4.9[f] | 31.1 | 10.0 | | | 1.3 | | 6.5 | 2.2 | 27.4 | 14.8 | 1.9 | 2051 |
| 1 | Leaf | HPLC | | 7.3[f] | 21.2 | 25.1 | | | 6.5 | | 1.5 | 1.9 | 13.7 | 17.4 | 5.4 | 2051 |
| 1 | Root | HPLC | | 6.4[f] | 51.2 | 11.9 | | | 3.3 | | 8.3 | 3.2 | 16.2 | 13.1 | 2.6 | 2051 |
| | Similar data reported for PC molecular species in cotyledon, leaf, hypocotyl, and root tissue of adzuki bean cell culture | | | | | | | | | | | | | | | 2052 |
| *Vigna unguiculata* (L.) Walp. (Cowpea) | | | | | | | | | | | | | | | | |
| 2 | Leaf, drought-resistant | HPLC | | | 26 | 24 | | | 4 | | 7 | | 15 | 18 | 6 | 2064 |
| | Leaf, drought-sensitive | HPLC | | | 9 | 41 | | | 16 | | 5 | | 3 | 12 | 13 | 2064 |
| *Zea mays* L. ssp. *saccharata* Sturt (Sweet Corn) | | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | | | 11 | 18 | | | | 14 | 32 | | 24 | 1 | | 2086 |

[a]Including 14:0/18:0.
[b]Including 18:2/18:2 (LL).
[c]Including 16:0/16:1.
[d]Including 18:1/16:1 PG.
[e]*sn*-1/*sn*-2 positions reversed.
[f]Including 18:0/18:2 (SL).
[g]Including 18:3/18:2 (LnL).
[h]Including 18:0/18:3 (SLn).

### Hydrolysis

Hydrolysis of DPPC with either HCl or NaOH in refluxing ethanol yields palmitic acid and a mixture of α- and β-glycerophosphoric acids owing to migration of the phosphate group. Under milder conditions (0.2*N* methanolic NaOH at 37 °C), the first-order rate constant for the liberation of palmitic acid is 1.0 $h^{-1}$. Most, if not all, of the free choline is formed by hydrolysis of the glycerophosphocholine ($k = 0.069$ $h^{-1}$) rather than the intact DPPC.[191] Hydrolysis of DPPC in acetate buffer at pH 4.0 follows pseudo-first-order kinetics ($k_{obs.} = 1.0 \times 10^{-2}$ $day^{-1}$ at 30 °C). The Arrhenius plot shows a break at the gel-to-liquid phase transition temperature $T_m$ (42 °C) with activation energy $E_a = 91$ kJ/mol below the $T_m$ and 67 kJ/mol above it.[2228]

Enzymatic hydrolysis of DPPC, DSPC, DOPC, or POPC with *Crotalus adamanteus* snake venom phospholipase [E.C. 3.1.1.4] gives exclusively the corresponding 2-lysophospholipids PHPC,[2134] SHPC,[2229] OHPC,[2230] and PHPC,[2230] whereas enzymatic hydrolysis of DPPC, POPC, DOPC, or DLPC with lipase from the mold *Rhizopus arrhizus* [E.C. 3.1.1.3] gives exclusively the corresponding 1-lysophospholipids HPPC,[2231] HOPC,[2232] HOPC,[2233] and HLPC,[2233] respectively. Both acyl groups of POPC are cleaved in 30 min and 37 °C with 1.0*N* aqueous methanolic NaOH.[2234]

## Lysophosphatidylcholines

### Physical Properties

1-Palmitoyl-*sn*-glycero-3-phosphocholine (PHPC), 16:0 LPC, $C_{24}H_{50}NO_7P$. *(R)-4,7-Dihydroxy-N,N,N-trimethyl-10-oxo-3,5,9-trioxa-4-phosphapentacosan-1-aminium Hydroxide, inner salt, 4-Oxide.*

PHPC [R.N. 17364-16-8]: *Hydrate*: mp 195-196 °C, $[\alpha]_D^{25}$ −2.2° ($CHCl_3$),[2231] readily soluble in methanol,[2216] critical micelle concentration.[2235] Spectra: Raman,[2236] $^1$H NMR and $^{31}$P NMR (figs.),[2237] $^{14}$N NMR,[2204] EI-MS (fig.),[2238] FAB-MS,[2135] FD-MS,[2177] CIMS (fig.),[2238] SIMS.[2239] Chromatography: PC,[2212] TLC,[2240] HPTLC,[1405] HPLC,[2216] silicic acid column.[2212] *rac*-PHPC [R.N. 17364-17-0]: Dec. 260-262 °C,[2241] IR (fig.),[2242] ESI-MS and ESI-MS/MS (figs.).[2243] $[CdCl_2]_3[PHPC.H_2O]_2$: Solid, insoluble in ether or ethanol.[2244]

2-Palmitoyl-*sn*-glycero-3-phosphocholine (HPPC), 16:0 LPC, $C_{24}H_{50}NO_7P$. *(R)-4-Hydroxy-7-hydroxymethyl-N,N,N-trimethyl-9-oxo-3,5,8-trioxa-4-phosphatetracosan-1-aminium Hydroxide, inner salt, 4-Oxide.*

HPPC [R.N. 66757-27-5; see also 80547-97-5]: Soluble in benzene, $CHCl_3$, DMSO and methanol. Chromatography: HPLC.[2216] *Hydrate*: Soluble in chloroform. Spectra: $^1$H and $^{31}$P NMR (figs.),[2237] ESI-MS/MS (fig.).[2243] Chromatography: PC,[2212] TLC,[2237] gel filtration.[2237]

1-Stearoyl-*sn*-glycero-3-phosphocholine (SHPC), 18:0 LPC, $C_{26}H_{54}NO_7P$. *(R)-4,7-Dihydroxy-N,N,N-trimethyl-10-oxo-3,5,9-trioxa-4-phosphaheptacosan-1-aminium Hydroxide, inner salt, 4-Oxide*

SHPC [R.N. 19420-57-6]: Readily soluble in methanol,[2216] insoluble in water.[2235] Spectra: IR,[2201] $^1$H NMR,[2201] FAB-MS,[2135] FD-MS (fig.),[2177] CI-MS/MS.[2245]

Chromatography: PC,[2197] HPLC,[2216] silicic acid column.[2197] *Hydrate*: Needles, mp 257.5-258.5 °C, $[\alpha]_D^{25}$ −2.87° ($CHCl_3$/MeOH).[2246] Spectra: $^{13}C$ and $^{31}P$ NMR,[2247] CI-MS.[2248] Chromatography: TLC.[2240]
$[CdCl_2]_3[SHPC.H_2O]_2$: Solid.[2230]
$[CdCl_2]_3[SHPC.HCl]_2$: Solid.[2197]

1-Oleoyl-*sn*-glycero-3-phosphocholine (OHPC), 18:1 LPC, $C_{26}H_{52}NO_7P$. *(R)-4,7-Dihydroxy-N,N,N-trimethyl-10-oxo-3,5,9-trioxa-4-phosphaheptacos-18-en-1-aminium Hydroxide, inner salt, 4-Oxide*

OHPC [R.N. 19420-56-5]: *Hydrate*, mp 240 °C, $[\alpha]_D^{20}$ −3.2 ($CHCl_3$/ethanol).[2230] Spectra: $^1H$ and $^{14}N$ NMR,[2204] FAB-MS,[2249] FD-MS,[2177] CI-MS,[2248] ESI-MS/MS (fig.).[2243] Chromatography: PC,[2250] TLC,[2250] HPLC,[2251] silicic acid column.[2197]
$[CdCl_2]_3[OHPC{\cdot}H_2O]_2$: Solid.[2197]

2-Oleoyl-*sn*-glycero-3-phosphocholine (HOPC), 18:1 LPC, $C_{26}H_{52}NO_7P$. *(R)-4-Hydroxy-7-hydroxymethyl-N,N,N-trimethyl-9-oxo-3,5,8-trioxa-4-phosphahexacos-17-en-1-aminium Hydroxide, inner salt, 4-Oxide.*

HOPC [R.N. 22248-65-3]: $[\alpha]_D^{25}$ +3.1° ($CHCl_3$/methanol).[2233] Spectra: ESI-MS/MS (fig.).[2243] Chromatography: TLC,[2233] gel filtration column.[2233]

1-Linoleoyl-*sn*-glycero-3-phosphocholine (LHPC), 18:2 LPC, $C_{26}H_{50}NO_7P$. *(R)-4,7-Dihydroxy-N,N,N-trimethyl-10-oxo-3,5,9-trioxa-4-phosphaheptacosa-18,21-dien-1-aminium Hydroxide, inner salt, 4-Oxide*

LHPC [R.N. 22252-07-9; see also 5655-12-9]. *Hydrate*: Spectra: IR,[2252] $^1H$ NMR,[2204] $^{13}C$ NMR,[2252] FD-MS.[2122] Chromatography: TLC, HPLC, silica gel column.[2252]

2-Linoleoyl-*sn*-glycero-3-phosphocholine (HLPC), 18:2 LPC, $C_{26}H_{50}NO_7P$. *(R)-4-Hydroxy-7-hydroxymethyl-N,N,N-trimethyl-9-oxo-3,5,8-trioxa-4-phosphahexacosa-17,20-dien-1-aminium Hydroxide, inner salt, 4-Oxide.*

HLPC [R.N. 27304-12-7; see also 3973-94-2]: Spectra: IR, $^1H$, and $^{13}C$ NMR, FAB-MS.[2252] Chromatography: TLC,[2233] HPLC,[2252] silicic acid column.[2252]

1-Linolenoyl-*sn*-glycero-3-phosphocholine (LnHPC), 18:3 LPC, $C_{26}H_{48}NO_7P$. *(R)-4,7-Dihydroxy-N,N,N-trimethyl-10-oxo-3,5,9-trioxa-4-phosphaheptacosa-18,21,24-trien-1-aminium Hydroxide, inner salt, 4-Oxide.*

LnHPC [R.N. 62512-91-8; see also 63163-01-9]: *Hydrate*: FD-MS.[2177]

2-Linolenoyl-*sn*-glycero-3-phosphocholine (HLnPC), 18:3 LPC, $C_{26}H_{48}NO_7P$. *(R)-4-Hydroxy-7-hydroxymethyl-N,N,N-trimethyl-9-oxo-3,5,8-trioxa-4-phosphahexacosa-17,20,23-trien-1-aminium Hydroxide, inner salt, 4-Oxide.*

HLnPC [R.N. 77667-11-9]: No data.

## Synthesis

PHPC may be prepared (a) by catalytic hydrogenation of 1-palmitoleyl-*sn*-glycero-3-phosphocholine,[2231] (b) by partial methanolysis of DPPC with octylamine in methanol,[2253] (c) by enzymatic hydrolysis of DPPC with snake venom phospholipase $A_2$,[2231]

(d) by acylation of *sn*-glycero-3-phosphocholine with palmitoyl chloride,[2212] or (e) by stepwise reaction of 2-benzyl-1-palmitoyl-*sn*-glycerol with 2-bromoethyl phosphorodichloridate and trimethylamine.[2240]

HPPC may be prepared (a) by enzymatic hydrolysis of DPPC with lipase from the mold *R. arrhizus*[2237] or (b) by oxidation of a 1-(alk-1′-enyl)-2-palmitoyl-*sn*-glycero-3-phosphocholine with iodine.[2254]

SHPC may be prepared (a) by partial acylation of *sn*-glycero-3-phosphocholine with stearoyl chloride,[2197] (b) by enzymatic hydrolysis of DSPC with snake venom phospholipase $A_2$,[2246] (c) by catalytic hydrogenation of OHPC,[2230] or (d) by stepwise reaction of 2-benzyl-1-stearoyl-*sn*-glycerol with 2-bromoethyl phosphorodichloridate and trimethylamine[2240] or with $POCl_3$ and choline *p*-toluene-sulfonate.[2255]

OHPC may be prepared (a) by partial acylation of *sn*-glycero-3-phosphocholine with oleoyl chloride,[2197] (b) by partial methanolysis of 2-acetyl-1-oleoyl-*sn*-glycero-3-phosphocholine with *t*-BuOK in methanol,[2240] or (c) by enzymatic hydrolysis of DOPC with snake venom phospholipase $A_2$.[2230]

HOPC may be prepared by enzymatic hydrolysis of POPC[2232] or DOPC[2233] with lipase from the mold *R. arrhizus*.

LHPC may be prepared (a) by stepwise reaction of 1-linoleoyl-2-methoxyethoxymethyl-*sn*-glycerol with $POCl_3$ and choline *p*-toluenesulfonate[2208] or (b) by migration of the linoleoyl group during the preparation of HLPC from soybean PC in phosphate buffer.[2252]

HLPC may be prepared by hydrolysis of DLPC with lipase from the mold *R. arrhizus*[2233] or of soybean PC with lipase from the fungus *Mucor javanicus*.[2252]

## Hydrolysis

The second-order rate constant for base-catalyzed hydrolysis of PHPC is about $1.8 \times 10^{-2}$ $M^{-1}$ $s^{-1}$ about 8500 times slower than the rate of acyl migration.[2237] PHPC, SHPC, and OHPC are rapidly hydrolyzed to *sn*-glycero-3-phosphocholine by *Penicillium notatum* phospholipase B.[2256] The rate of hydrolysis of HPPC to *sn*-glycero-3-phosphocholine by this phospholipase is about 15 times slower than that of PHPC.[2254] PHPC and SHPC are rapidly hydrolyzed to PHPA and SHPA, respectively, by Savoy cabbage phospholipase D.[2257]

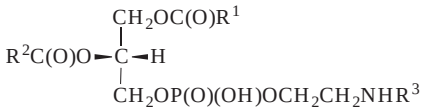
## Migration

PHPC gradually rearranges in aqueous solution to an equilibrium mixture containing 90% PHPC and 10% HPPC. The second-order rate constant for the migration of the palmitoyl group from *sn*-2 to *sn*-1 is about 160 $M^{-1}$/s for base-catalyzed migration (pH 6.2-9) and $4 \times 10^{-4}$ $M^{-1}$/s for acid-catalyzed migration (pH 1-2). Migration of the phosphoryl group is observed only at pH 1 or below.[2237]

Migration of the linoleoyl group from *sn*-2 to *sn*-1 occurs during the preparation of HLPC in phosphate buffer resulting in a mixture containing 94% HLPC and 6% LHPC, but can be prevented by the use of borate buffer.[2252]

# PHOSPHATIDYLETHANOLAMINES

This group comprises the phosphatidylethanolamines (PE), the lysophosphatidylethanolamines (LPE), the *N*-acylphosphatidylethanolamines (NAPE), and the *N*-acyllysophosphatidylethanolamines (NALPE):



PE, $R^1 = R^2 =$ alkyl, $R^3 = H$
1-LPE, $R^1 = R^3 = H$, $R^2 =$ alkyl
2-LPE, $R^1 =$ alkyl, $R^2 = R^3 = H$
NAPE, $R^1 = R^2 = R^3 =$ alkyl
1-NALPE, $R^1 = H$, $R^2 = R^3$ ′ alkyl
2-NALPE, $R^1 = R^3 =$ alkyl, $R^2 = H$

## Phosphatidylethanolamines

### Physical Properties

1,2-Dipalmitoyl-*sn*-glycero-3-phospho-1′-ethanolamine (DPPE), 16:0/16:0 PE, $C_{37}H_{74}NO_8P$. *(R)-Hexadecanoic Acid, 1-[[[(2-aminoethoxy)hydroxyphosphinyl]oxy] methyl]-1,2-ethanediyl Ester.*

DPPE [R.N. 923-61-5]: Microscopic spherulites (photo), mp 172.5-175 °C, $[\alpha]_D^{26}$ +6.4° ($CHCl_3$), soluble in $CHCl_3$, moderately soluble in ethanol, insoluble in acetone, ether, benzene, petroleum ether[2258]; ORD,[2147] DSC,[2259] TGA,[1367] IR dichroism.[2260] Spectra: IR (fig.),[2258] FTIR,[2261] Raman (fig.),[2262] $^1$H NMR,[222] $^{13}$C and $^{31}$P NMR (figs.),[2210] FAB-MS,[2249] FD-MS,[2263] CI-MS,[2264] LSIMS,[2154] FAB-MS/MS,[2136] CID-MS/MS (fig.).[2265] X-ray.[2258] Chromatography: TLC,[2266] HPTLC,[1405] HPLC,[2239] LC-MS,[2154] GFC,[2267] SFC.[2156] *Dihydrate*: Crystals, $^{13}$C and $^{31}$P CP-MAS-NMR (figs.), two conformations.[2169]

1-Palmitoyl-2-oleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (POPE), 16:0/18:1 PE, $C_{39}H_{76}NO_8P$. *[R-(Z)]-9-Octadecenoic Acid, 1-[[[(2-Aminoethoxy)hydroxyphosphinyl]oxy] methyl]-2-[(1-oxo-hexadecyl)oxy]ethyl Ester.*

POPE [R.N. 39749-44-5]: Colorless waxy solid, mp 184-185 °C[2268]; CE (fig.),[2181] MALDI FT-ICR-MS/MS (fig.).[1370] *Monohydrate*: Hard fatty wax, mp 194.6 °C, $[\alpha]_D^{22}$ +6.35° ($CHCl_3$), soluble in $CHCl_3$ and methanol, insoluble in ether or acetone,[2269] DSC.[2227] Spectra: FTIR,[2270] $^{31}$P NMR (fig.),[2227] 2D-[$^1$H][$^{31}$P]-NMR,[2271] FAB-MS,[2135] LSIMS (fig.),[2139] FAB-MS/MS,[2272] CID-MS/MS (fig.),[2265] Chromatography: HPLC,[2100] LC-MS.[2273] Electrophoresis: PE.[2100]

1-Palmitoyl-2-linoleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (PLPE), 16:0/18:2 PE, $C_{39}H_{74}NO_8P$. *[R-(Z,Z)]-9,12-Octadecadienoic Acid, 1-[[[(2-aminoethoxy) hydroxyphosphinyl]oxy]methyl]-2-[(1-oxohexadecyl)oxy]ethyl Ester.*

PLPE [R.N.26662-95-3; see also 14018-09-8]: Pale yellow oil. Spectra: IR,[1787] $^1$H and $^{13}$C NMR,[2274] EI-MS,[1787] FAB-MS,[1787] CI-MS,[2264] CID-MS/MS (fig.).[2265] Chromatography: TLC,[1787] HPLC,[2100] HPLC/CI-MS,[2180] LC/MS,[2273] LC/MS/MS (fig.).[1415]

PLPE.HCl [R.N. 106498-49-1]: Colorless waxy solid, mp 155 °C, $[\alpha]_D^{20}$ +6.0° ($CHCl_3$), TLC.[2275]

1-Palmitoyl-2-linolenolyl-*sn*-glycero-3-phospho-1′-ethanolamine (PLnPE), 16:0/18:3 PE, $C_{39}H_{72}NO_8P$. *[R-(Z,Z,Z)]-9,12,15-Octadecatrienoic Acid, 1-[[[(2-Aminoethoxy) hydroxyphosphinyl]oxy]methyl]-2-[(1-oxohexadecyl)oxy]ethyl Ester.*

PLnPE [R.N. 4009-43-2]: White powder, $[\alpha]_D^{20}$ +6.0° ($CHCl_3$), IR, TLC,[2276] HPLC.[2132]

1-Stearoyl-2-oleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (SOPE), 18:0/18:1 PE, $C_{41}H_{80}NO_8P$. *[R-(Z)]-9-Octadecenoic Acid, 1-[[[(2-Aminoethoxy)hydroxyphosphinyl]oxy] methyl]-2-[(1-oxooctadecyl)oxy]ethyl Ester.*

SOPE [R.N. 6418-95-7]: White solid,[2277] mp 189-190 °C, $[\alpha]_D^{20}$ +6.1° ($CHCl_3$), soluble in chloroform and ether, fairly soluble in acetone, less soluble in ethanol, insoluble in water[2188]; monolayer film properties.[2191] Spectra: IR (fig.),[2188] FAB-MS,[2135] FD-MS.[2122] Chromatography: PC,[2277] TLC,[2278] HPLC,[2110] MPLC,[2278] silicic acid column,[2188] LC-MS (fig.).[2187] *rac*-SOPE, Na salt [R.N. 78524-86-4]: DTA (fig), X-ray,[2279] $^1$H NMR.[2280]

1-Stearoyl-2-linoleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (SLPE), 18:0/18:2 PE, $C_{41}H_{78}NO_8P$. *[R-(Z,Z)]-9,12-Octadecadienoic Acid, 1-[[[(2-Aminoethoxy) hydroxyphosphinyl]oxy]methyl]-2-[(1-oxooctadecyl)oxy]ethyl Ester.*

SLPE [R.N. 7266-53-7]: DSC (fig.),[2281] monolayer film properties,[2191] FAB-MS,[2135] HPLC.[2100] *S*-SLPE: $[\alpha]_D^{20}$ −6.0° ($CHCl_3$), IR, PC, TLC, silicic acid chromatography.[2282]

1-Stearoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-ethanolamine (SLnPE), 18:0/18:3 PE, $C_{41}H_{76}NO_8P$. *[R-(Z,Z,Z)]-9,12,15-Octadecatrienoic Acid, 1-[[[(2-Aminoethoxy) hydroxyphosphinyl]oxy]methyl]-2-[(1-oxooctadecyl)oxy]ethyl Ester.*

SLnPE [R.N. 61177-33-1]: HPLC,[2110] monolayer film properties.[2191]

1,2-Dioleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (DOPE), 18:1/18:1 PE, $C_{41}H_{78}NO_8P$. *[R-(Z,Z)]-9-Octadecenoic Acid, 1-[[[(2-aminoethoxy)hydroxyphosphinyl]oxy]methyl]-1,2-ethanediyl Ester.*

DOPE [R.N. 4005-05-1]: Almost white, waxy, slightly hygroscopic solid,[2283] mp 195-200 °C,[2270] soluble in $CHCl_3$, ether and petroleum ether, somewhat soluble in methanol (20.2 g/100 mL) or ethanol (13.2 g/100 mL), and sparingly soluble in acetone (2.6 g/100 mL),[2283] $[\alpha]_D^{20}$ +6.0° ($CHCl_3$),[2283] DSC,[2284] TGA,[1367] monolayer film properties.[2191] Spectra: IR (fig.),[2283] FTIR,[2270] $^1$H NMR,[2285] $^{13}$C NMR,[2201] $^{31}$P NMR (fig.),[2286] 2d-[$^1$H] [$^{13}$C]-NMR (fig.),[2174] FD-MS,[2122] LSIMS,[2239] MALDI FT-ICR/MS (fig.).[1370] Chromatography: TLC,[2166] HPLC,[2100] LC-MS,[1415] silicic acid column.[2283]

1-Oleoyl-2-linoleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (OLPE), 18:1/18:2 PE, $C_{41}H_{76}NO_8P$. *[R-(Z,Z,Z)]-9,12-Octadecadienoic Acid, 1-[[[(2-Aminoethoxy) hydroxyphosphinyl]oxy]methyl]-2-[(1-oxo-9-octadecenyl)oxy]ethyl Ester.*

OLPE [R.N. 1188-56-3]: $[\alpha]_D^{25}$ +4.1° ($CHCl_3$), soluble in chloroform and ether.[2287] Chromatography: TLC,[2287], HPLC,[2100] silicic acid column.[2287] *rac-OLPE*: IR, PC.[2288]

1-Oleoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-ethanolamine (OLnPE), 18:1/18:3 PE, $C_{41}H_{74}NO_8P$. *[R-(all Z)]-9,12,15-Octadecatrienoic Acid, 1-[[[(2-Aminoethoxy) hydroxyphosphi-nyl]oxy]methyl]-2-[(1-oxo-9-octadecenyl)oxy]ethyl Ester.*

OLnPE [R.N. 124265-78-7] HPLC.[1892]

1,2-Dilinoleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (DLPE), 18:2/18:2 PE, $C_{41}H_{74}NO_8P$. *[R-(all Z)]-9,12-Octadecadienoic Acid, 1-[[[(2-aminoethoxy) hydroxyphosphinyl]oxy]methyl]-1,2-ethanediyl Ester.*

DLPE [R.N. 20707-71-5]: Soft wax, mp 25 °C,[2268] soluble in chloroform, ether, and petroleum ether, less soluble in ethanol, poorly soluble in acetone; forms a stable emulsion with water,[2289] $[\alpha]_D^{20}$ +6.0° ($CHCl_3$),[2290] DSC,[2227] TGA.[1367] Spectra: IR (fig.),[2289] $^{31}P$ NMR.[2227] Chromatography: PC,[2290] TLC,[2289] HPLC,[2100] DEAE-celullose column,[2291] silicic acid column,[2290] LC-MS (fig.).[2273]

1-Linoleoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-ethanolamine (LLnPE), 18:2/18:3 PE, $C_{41}H_{72}NO_8P$. *[R-(all Z)]-9,12,15-Octadecatrienoic Acid, 1-[[[(2-Aminoethoxy) hydroxyphosphinyl]oxy]methyl]-2-[(1-oxo-9,12-octadecadienyl)oxy]ethyl Ester.*

LLnPE [R.N. 124264-80-8]: HPLC.[2100]

1,2-Dilinolenoyl-*sn*-glycero-3-phospho-1′-ethanolamine (DLnPE), 18:3/18:3 PE, $C_{41}H_{70}NO_8P$. *[R-(all Z)]-9,12,15-Octadecatrienoic Acid, 1-[[[(2-Aminoethoxy) hydroxyphosphinyl]oxy]methyl]-1,2-ethanediyl Ester.*

DLnPE [R.N. 34813-40-6]: $[\alpha]_D$ +6.1° ($CHCl_3$),[2292] DSC.[2227] Spectra: IR,[2292] $^{31}P$ NMR.[2227] Chromatography: HPLC,[2100] LC-MS.[2273] *rac*-DLnPE: PC.[2288]

## Molecular Species Composition

The molecular species composition of phosphatidylethanolamine in plants, determined by any of the methods described on pages 168–171, is given in Table 4-9.

## Synthesis

DPPE may be prepared (a) by phosphorylation of 1,2-dipalmitoyl-*sn*-glycerol with phenyl phosphorodichloridate,[2258] $PCl_3$/imidazole,[2211] or methyl *N*,*N*-diisopropylaminophosphorochloridite,[2210] followed by reaction with *N*-BOC-ethanolamine or *N*-tritylethanolamine, (b) by phosphorylation of 1,2-dipalmitoyl-*sn*-glycerol with 2-phthalimidoethyl phosphorodichloridate,[2266] 2-phthalimidoethyl dihydrogen phosphate,[2266] or 2-chloro-2-oxo-1,3,2-dioxaphospholane and trimethylamine,[2223] (c) by acylation of *sn*-glycero-3-phospho-*N*-phthaloylethanolamine[2293,2294] or polymer-supported *sn*-glycero-3-phospho-*N*-tritylethanolamine[2295] with palmitoyl chloride or palmitic anhydride, or (d) by condensation of 1,2-dipalmitoyl-*sn*-glycero-3-bromohydrin[2296] or -3-iodohydrin[2297] with silver phenyl 2-BOC-aminoethyl phosphate or silver benzyl 2-tritylaminoethyl phosphate.

POPE may be prepared (a) by condensation of 1-palmitoyl-2-oleoyl-*sn*-glycero-3-iodohydrin with silver *t*-butyl 2-(*N*-*t*-butoxycarbonyl)aminoethyl phosphate[2269] or of 2-tritylaminoethyl iodide with silver 1-palmitoyl-2-oleoyl-*sn*-glycero-3-(*p*-nitrobenzyl phosphate),[2268] (b) by condensation of 1-palmitoyl-2-oleoyl-*sn*-glycero-3-(dihydrogen phosphate) with *N*-BOC-ethanolamine in the presence of 2,4,6-triisopropylbenzenesulfonyl chloride,[2298] (c) by stepwise acylation of 1-trityl-*sn*-glycero-3-phospho-*N*-tritylethanolamine with oleoyl imidazolide and palmitic

**Table 4-9** Molecular Species Composition: Phosphatidylethanolamines (mol%)

| No. | Plant part | Method | 16:0 16:0 | 16:0 18:1 | 16:0 18:2 | 16:0 18:3 | 18:0 18:1 | 18:0 18:2 | 18:0 18:3 | 18:1 18:1 | 18:1 18:2 | 18:1 18:3 | 18:2 18:2 | 18:2 18:3 | 18:3 18:3 | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Arabidopsis thaliana* (L.) Heynh (Mouse-Ear Cress) | | | | | | | | | | | | | | | | |
| 1 | Leaf plasma membrane | GLC | 0.6[a] | 0.8 | 43.0 | 21.0 | 0.4 | 1.5 | Trace | 1.2 | 2.4 | 14.8[b] | | 8.6 | 1.6 | 1478 |
| *Avena sativa* L. (Oats) | | | | | | | | | | | | | | | | |
| 1 | Leaf plasma membrane | GLC | 1.2[a] | 2.1 | 48.4 | 18.0 | 0.3 | | 0.2 | 0.7 | 1.8 | 14.8[b] | | 8.5 | 2.6 | 1502 |
| 1 | Root plasma membrane | GLC | | | 63 | 14 | | | | | | | 17 | 6 | | 2113 |
| *Brassica napus* L. (Rape, low erucic acid (Canola)) | | | | | | | | | | | | | | | | |
| 1 | Leaf | HPLC | | | 21.1 | 23.3 | | | 4.2 | | | | 14.5 | 25.3 | 11.6 | 2117 |
| *Camellia sinensis* L. (Tea) | | | | | | | | | | | | | | | | |
| 1 | Pollen | HPLC | | | | 66 | | | | | | | | | 23 | 1558 |
| *Daucus carota* L. (Carrot) | | | | | | | | | | | | | | | | |
| 1 | Cell culture | AgTLC | | 2.2 | 48.0 | | | | | | 9.7 | | 33.4 | 6.7 | | 1648 |
| *Dianthus caryophyllus* L. (Carnation) | | | | | | | | | | | | | | | | |
| 1 | Flower microsomal membr. | GLC | | 2.4 | 73.5 | | | 0.2 | | | 1.0 | 3.2 | 19.6 | | | 1652 |
| *Diptychocarpus strictus* (Fisch.) Trautv. | | | | | | | | | | | | | | | | |
| 1 | Seed | 1R,2R | 1.1 | 4.5 | 8.0 | 10.0 | 0.4 | 0.7 | 1.0 | 5.6 | 9.0 | 16.0 | 6.5 | 9.0 | 6.4 | 959 |
| *Echium plantagineum* L. (Salvation Jane) | | | | | | | | | | | | | | | | |
| 1 | Leaf | AgTLC | | | 18 | 18 | | | | | 2[c] | 5[c] | 9.5 | 5.5[c] | 2 | 2120 |
| *Glycine max* (L.) Merr. (Soybean) | | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | 0.2 | 7.4[d] | 32.9 | 4.2 | 0.7 | | 0.8 | 1.8 | 8.1 | 2.0 | 33.1 | 8.2 | 0.6 | 1693 |
| 1 | Seed | FD-MS | | 4.3 | 38.3 | 5.8 | | | | 4.6[d] | 9.9[e] | | 29.0 | 8.1 | | 2134 |
| 1 | Seed | CI-MS | | 5.6 | 44.0 | 2.5 | 0.7 | | | 7.0[d] | 11.3[e] | | 24.1 | 3.3 | 1.4 | 2123 |
| 1 | –, hypocotyl | AgTLC | | | 42 | 7 | | 6 | | | 4 | | 23 | 16 | Trace | 1690 |
| 1 | –, cotyledon | AgTLC | | | 52 | 1 | | 8 | | | 10 | | 20 | 4 | Trace | 1690 |
| 1 | Seedling, microsomes | HPLC | | 3.4 | 31.6 | 4.6 | | 5.8 | Trace | Trace | 6.5 | 1.7 | 38.0 | 8.4[c] | | 2125 |

[a]Including 14:0/18:0; [b]Including 18:2/18:2 (LL); [c]*sn*-1/*sn*-2 positions reversed; [d]Including 18:0/18:2 (SL); [e]Including 18:0/18:3 (SLn); [f]Including 18:3/18:2 (LnL); [g]Including 18:1/18:1 (OO).

*Continued*

**Table 4-9** Molecular Species Composition: Phosphatidylethanolamines (mol%)—cont'd

| No. | Plant part | Method | 16:0 16:0 | 16:0 18:1 | 16:0 18:2 | 16:0 18:3 | 18:0 18:1 | 18:0 18:2 | 18:0 18:3 | 18:1 18:1 | 18:1 18:2 | 18:1 18:3 | 18:2 18:2 | 18:2 18:3 | 18:3 18:3 | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Gossypium barbadense* L. (Sea Island Cotton) | | | | | | | | | | | | | | | | |
| 1 | Seed kernel | 1R,2R | 0.9 | 9.2 | 39.0 | | 0.5 | 2.1 | | 1.5 | 6.0 | | 28.0 | | | 1709 |
| *Gossypium hirsutum* L. (Upland Cotton) | | | | | | | | | | | | | | | | |
| 1 | Seed | FAB-MS/MS | | | +++ | | | | | | | | + | | | 2311 |
| 1 | Seed kernel | 1R,2R | 2.2 | 7.2 | 38.3 | | 0.3 | 1.9 | | 0.7 | 3.5 | | 26.4 | | | 1374 |
| *Hibiscus cannabinus* L. (Kenaf) | | | | | | | | | | | | | | | | |
| 1 | Seed | 1R,2R | 1.6 | 11.4 | 25.5 | 0.4 | 0.8 | 1.7 | | 3.6 | 8.1 | 0.1 | 24.1 | 0.4 | | 1377 |
| *Lavandula vera* DC (English Lavender) | | | | | | | | | | | | | | | | |
| 1 | Cell culture | AgTLC | | 10.4 | 12.4 | 18.7 | 6.9 | 4.9 | 15.7 | 3.5 | 2.0 | 11.4 | 1.5 | 2.0 | 4.4 | 1765 |
| *Lilium longiflorum* Thunb. (Trumpet Lily) | | | | | | | | | | | | | | | | |
| 1 | Pollen | HPLC | 1.0 | | 20.3 | 39.3 | | | | | | | 6.8 | 16.2[f] | 9.1 | 1769 |
| *Lycopersicon esculentum* Mill. (Tomato) | | | | | | | | | | | | | | | | |
| 1 | Fruit, pericarp | GLC | 1.8 | 1.8 | 53.4 | 4.5 | | | | | | | 19.4 | 0 | 4.1 | 2128 |
| *Nicotiana tabacum* L. (Tobacco) | | | | | | | | | | | | | | | | |
| 1 | Cell culture | AgTLC | | Trace | 67.4 | 13.2 | | | 10.5 | | Trace | Trace | 8.9 | Trace | | 1495 |
| *Oryza sativa* L. (Rice) | | | | | | | | | | | | | | | | |
| 1 | Bran, glutinous | AgTLC | | 21.1 | 33.4 | | (18:2/18:1, 7.0) | | | 5.6 | 13.6 | | 19.3 | | | 1845 |
| 1 | Bran, glutinous | 1R,2R | | 17.6 | 30.8 | | (18:2/18:1, 10.0) | | | 6.6 | 11.5 | | 17.4 | | | 1845 |
| 1 | Bran, nonglutinous | AgTLC | | 16.1 | 38.3 | | (18:2/18:1, 7.6) | | | 6.5 | 14.2 | | 17.3 | | | 1845 |
| 1 | Bran, nonglutinous | 1R,2R | | 13.8 | 38.4 | | (18:2/18:1, 7.0) | | | 4.1 | 11.3 | | 19.5 | | | 1845 |
| *Perilla frutescens* (L.) Britt. (Perilla Mint) | | | | | | | | | | | | | | | | |
| 1 | Seed | AgTLC | | | | | 1.7 | 20.9[g] | | | 26.3[e] | 14.8[b] | | 22.6 | 13.7 | 2094 |
| 1 | Seed | 1R,2R | | | | | 2.3 | 17.6[g] | | | 28.5[e] | 16.0[b] | | 19.8 | 15.6 | 2094 |
| *Phaseolus coccineus* L. (Scarlet Runner Bean) | | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | 0.3 | 6.9[d] | 34.6 | 20.1 | <0.1 | | 0.6 | 0.8 | 5.3 | 3.7 | 12.6 | 11.8 | 3.3 | 1693 |
| *Phaseolus vulgaris* L. (Kidney Bean) | | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | 0.7 | 10.4[d] | 23.9 | 23.7 | 0.5 | | 1.5 | 2.0 | 7.3 | 6.1 | 7.6 | 11.0 | 5.3 | 1693 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Picea abies* (L.) Karst. (Spruce) | | | | | | | | | | | | | | | |
| 1 | Shoot | GLC | 6.0 | 3.6 | 35.6 | 0.6 | | 6.0 | | 3.6 | 2.7 | | 28.5 | | | 2115 |
| *Pinus nigra* Arnold (Black Pine) | | | | | | | | | | | | | | | |
| 1 | Needle (leaf) | HPLC | 1 | <1 | 14 | 10 | | 1 | | | 1 | 11 | 5 | 2 | 1 | 1892 |
| *Pisum sativum* L. (Pea) | | | | | | | | | | | | | | | |
| 1 | Seed | AgTLC | | 28.6 | 14.1 | | 8.3 | | | 10.3 | 14.4 | | 24.3 | | | 1904 |
| 1 | Seed | HPLC | 0.1 | 16.4[d] | 21.7 | 1.4 | 2.6 | | 0.6 | 8.1 | 21.9 | 1.8 | 22.1 | 2.6 | 0.5 | 1693 |
| 1 | Leaf | HPLC | | 1.3 | 36.8 | 13.1 | Trace | 5.2 | 4.7 | | 2.1 | | 19.6 | 13.4[c] | 2.4 | 2125 |
| *Raphanus sativus* L. (Radish) | | | | | | | | | | | | | | | |
| 1 | Seedling | HPLC | 6.1 | 3.1 | 21.8 | 27.0 | | 3.1 | 3.5 | | 6.5 | 7.3 | 9.2 | 11.0 | 4.5 | 2131 |
| *Rauvolfia serpentina* Benth ex Kurz (Indian Snakeroot) | | | | | | | | | | | | | | | |
| 1 | Cell culture | AgTLC | | | 59.1 | 2.7 | Trace | 4.6 | 0.5 | 0.4 | | | 32.7 | | | 1495 |
| *Secale cereale* L. (Rye) | | | | | | | | | | | | | | | |
| 2 | Grain (1) | HPLC | | 4 | 34 | 3 | | | | 2 | 11 | 2 | 33 | 10 | 1 | 1957 |
| | Grain (2) | | | 4 | 28 | 4 | | | | 2 | 11 | 3 | 36 | 11 | 1 | 1957 |
| 1 | Leaf plasma membrane | GLC | 1.2[a] | 2.2 | 39.1 | 22.0 | 0.4 | | Trace | 0.4 | 0.9 | 14.6[b] | | 11.7 | 4.7 | 1502 |
| *Solanum tuberosum* L. (Potato) | | | | | | | | | | | | | | | |
| 1 | Tuber | HPLC | | | 38.2 | 9.1 | | 7.1 | | | | | 34.4 | 11.1 | | 1410 |
| *Triticum aestivum* L. (Wheat) | | | | | | | | | | | | | | | |
| 1 | Flour | AgTLC | | 4.5 | 22.9 | 1.4 | 0.1 | 2.2 | | 1.1 | 7.3 | 0.4 | 44.3 | (18:2/18:1, 6.3) | | 2023 |
| 1 | Flour | 1R,2R | 1.3 | 3.2 | 23.3 | 1.4 | 0.3 | 2.1 | 0.1 | 1.0 | 7.1 | 0.4 | 43.9 | 2.6 | 0.1 | 2023 |
| *Vicia faba* L. (Broad Bean) | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | 0.4 | 13.3[d] | 26.0 | 3.6 | 2.6 | | 1.0 | 7.5 | 20.3 | 1.2 | 21.5 | 2.1 | 0.4 | 1693 |
| *Vigna angularis* (Willd.) Ohwi and Ohashi (Adzuki Bean) | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | | 3.8[d] | 46.3 | 14.6 | | | 1.5 | | 3.2 | 0.8 | 19.2 | 9.6 | 1.1 | 2051 |
| 1 | Leaf | HPLC | | 5.0[d] | 33.4 | 24.7 | | | 3.6 | | 1.0 | 0.7 | 13.4 | 14.8 | 3.3 | 2051 |
| 1 | Root | HPLC | | 2.1[d] | 71.2 | 9.1 | | | 1.9 | | 2.3 | 0.9 | 6.3 | 5.7 | 0.5 | 2051 |
| | Similar data reported for PE molecular species in cotyledon, leaf, hypocotyl and root tissue of adzuki bean cell culture | | | | | | | | | | | | | | | 2052 |
| *Zea mays* L. ssp. *saccharata* Sturt (Sweet Corn) | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | | 6 | 23 | | | | | 5 | 26 | | 39 | 1 | | 2086 |

[a]Including 14:0/18:0.
[b]Including 18:2/18:2 (LL).
[c]*sn*-1/*sn*-2 positions reversed.
[d]Including 18:0/18:2 (SL).
[e]Including 18:0/18:3 (Sln).
[f]Including 18:3/18:2 (LnL).
[g]Including 18:1/18:1 (OO).

anhydride,[2278] (d) by the reaction of 1-palmitoyl-2-oleoyl-*sn*-glycero-3-(2-bromoethyl hydrogen phosphate) with ammonia,[2299] or (e) by reaction of POPC with ethanolamine in the presence of phospholipase D.[2227]

PLPE may be prepared (a) by condensation of 1-palmitoyl-2-linoleoyl-*sn*-glycero-3-iodohydrin with silver *p*-nitrobenzyl *N*-BOC-2-aminoethyl phosphate,[2275] (b) by acylation of *O*-methyl-1-palmitoyl-*sn*-glycero-3-phospho-(*N*-BOC)ethanolamine with linoleic acid in the presence of DCC,[2274] or (c) by reaction of PLPC with ethanolamine in the presence of phospholipase D.[2264] PLnPE may be prepared by condensation of 1-palmitoyl-2-linolenoyl-*sn*-glycerol 3-iodohydrin with silver benzyl 2-phthalimidoethyl phosphate.[2276]

SOPE may be prepared (a) by phosphorylation of 1-stearoyl-2-oleoyl-*sn*-glycerol with $POCl_3$ and quinoline followed by reaction with *N*-(2-hydroxyethyl)phthalimide,[2277] (b) by condensation of silver benzyl 1-stearoyl-2-oleoyl-*sn*-glycerol-3-phosphate with 2-iodoethylphthalimide,[2188] or (c) by stepwise acylation of 1-trityl-*sn*-glycero-3-phospho-*N*-tritylethanolamine with oleoyl imidazolide and stearic anhydride.[2278]

SLPE: None reported, but syntheses of the corresponding D- and DL-isomers are available.[2282,2288]

SLnPE may be prepared by condensation of 1-stearoyl-2-linolenoyl-*sn*-glycerol 3-iodohydrin with silver benzyl 2-tritylaminoethyl phosphate.[2300]

DOPE may be prepared (a) by phosphorylation of 1,2-dioleoyl-*sn*-glycerol with $POCl_3$/quinoline followed by reaction with *N*-(2-hydroxyethyl)phthalimide,[2283] (b) by acylation of *N*-phthaloyl-*sn*-glycero-3-phosphoethanolamine with oleoyl chloride[2301] or oleic anhydride[2302] or of *N*-trityl-*sn*-glycero-3-phosphoethanolamine with *N*-oleoylimidazole,[2201] (c) by condensation of 1,2-dioleoyl-*sn*-glycero-3-(2,2,2-tribromoethyl hydrogen phosphate) with *N*-tritylethanolamine in the presence of 2,4,6-triisopropylbenzenesulfonyl chloride,[2285] (d) by condensation of silver benzyl 1,2-dioleoyl-*sn*-glycero-3-phosphate with 2-tritylaminoethyl iodide,[2297] or (e) by reaction of DOPC with ethanolamine in the presence of phospholipase D.[2286]

OLPE may be prepared (a) by phosphorylation of 1-oleoyl-2-linoleoyl-*sn*-glycerol with $POCl_3$/quinoline followed by *N*-(2-hydroxyethyl) phthalimide[2287] or (b) by stepwise acylation of *N*-phthaloyl-*sn*-glycero-3-phosphoethanolamine with oleoyl chloride and linoleoyl chloride in the presence of pyridine.[2303]

DLPE may be prepared (a) by phosphorylation of 1,2-dilinoleoyl-*sn*-glycerol with 2-phthalimidoethyl phosphorodichloridate[2290] or *N*-(2,2,2-trichloroethoxycarbonyl)-2-aminoethyl phosphorodichloridate,[2291] (b) by acylation of *N*-phthaloyl-*sn*-glycero-3-phosphoethanolamine with linoleoyl chloride,[2289] (c) by condensation of 1,2-dilinoleoyl-*sn*-glycero-3-iodohydrin with silver benzyl 2-(*N*-tritylaminoethyl) phosphate[2268] or (e) by reaction of DLPC with ethanolamine in the presence of phospholipase D.[2227]

DLnPE may be prepared (a) by phosphorylation of 1,2,-dilinolenoyl-*sn*-glycerol with $POCl_3$/quinoline followed by *N*-BOC-ethanolamine,[2292] (b) by condensation of 1,2-dilinolenoyl-*sn*-glycero-3-phosphate with *N*-BOC-ethanolamine in the presence of trichloroacetonitrile,[2292] or (c) by reaction of DLnPC with ethanolamine in the presence of phospholipase D.[2227]

### Hydrolysis

Hydrolysis of DPPE in acetate buffer at pH 4.0 follows pseudo-first-order kinetics ($k_{obs} = 0.7 \times 10^{-2}$ day$^{-1}$ at 30 °C). There is a tendency toward faster degradation in the order DPPC < DPPC < DPPG.[2228] Upon saponification, DOPE yields 95% of the theoretical amount of oleic acid, showing that no conversion to elaidic acid has occurred.[2283] Methanolysis with HCl yields methyl oleate of 95-97% purity.[2302] Methanolysis of DLPE with $BF_3$/methanol yields about 98% methyl linoleate based on GC analysis.[2291]

## Lysophosphatidylethanolamines

### Physical Properties

1-Palmitoyl-*sn*-glycero-3-phospho-1′-ethanolamine (PHPE), 16:0 LPE, $C_{21}H_{44}NO_7P$. *(R)-Hexadecanoic Acid, 3-[[(2-aminoethoxy)hydroxyphosphinyl]oxy]-2-hydroxypropyl Ester.*
PHPE [R.N. 53862-35-4]: DSC.[2304] Spectra: Raman (fig.),[2304] $^1$H NMR,[2305] $^{31}$P NMR (fig.),[2304] FAB-MS,[2135] FD-MS (fig.),[2177] CI-MS (fig.),[2248] ESI-MS/MS (fig.),[2243] CID-MS/MS.[2265] Chromatography: TLC,[2240] HPTLC,[1405] silica gel column.[2305] $_{DL}$-PHPE [R.N. 19805-23-3]: Monoclinic crystals, mp 212 °C, X-ray,[2306] PC.[2297]

2-Palmitoyl-*sn*-glycero-3-phospho-1′-ethanolamine (HPPE), 16:0 LPE, $C_{21}H_{44}NO_7P$. *(R)-Hexadecanoic Acid, 2-[[(2-aminoethoxy)hydroxyphosphinyl]oxy]-1-(hydroxymethyl)ethyl Ester.*
HPPE [R.N. 19805-25-5]: Crystals, mp 220 °C, soluble in chloroform and hot ethanol. Chromatography: PC, TLC.[2297]

1-Stearoyl-*sn*-glycero-3-phospho-1′-ethanolamine (SHPE), 18:0 LPE, $C_{23}H_{48}NO_7P$. *(R)-Octadecanoic Acid, 3-[[(2-aminoethoxy)hydroxyphosphinyl]oxy]-2-hydroxypropyl Ester.*
SHPE [R.N. 69747-55-3]: DSC.[2304] Spectra: IR,[2201] $^1$H NMR,[2201] FAB-MS.[2135] Chromatography: TLC, silicic acid column.[2201]

1-Oleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (OHPE), 18:1 LPE, $C_{23}H_{46}NO_7P$. *[R-(Z)]-9-Octadecenoic Acid, 3-[[(2-aminoethoxy)hydroxyphosphinyl]oxy]-2-hydroxypropyl Ester.*
OHPE [R.N. 89576-29-4]: White waxy plates, mp 202-204 °C dec., $[\alpha]_D^{20}$ −2.5° ($CHCl_3$).[2307] Spectra: IR (fig.),[2307] $^1$H and $^{31}$P NMR (fig.),[2308] FAB-MS,[2135] FD-MS,[2177] X-ray.[2308] ESI-MS/MS (fig.),[2243] Chromatography: TLC,[2307] silica column,[2308] CM-cellulose column.[2308]

2-Oleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (HOPE), 18:1 LPE, $C_{23}H_{46}NO_7P$. *[R-(Z)]-9-Octadecenoic Acid, 2-[[(2-aminoethoxy)hydroxyphosphinyl]oxy]-1-(hydroxymethyl)ethyl Ester.*
HOPE [R.N. 60701-97-5]: ESI-MS/MS.[2243]

1-Linoleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (LHPE), 18:2 LPE, $C_{23}H_{44}NO_7P$. *[R-(Z,Z)]-9,12-Octadecadienoic Acid, 3-[[(2-aminoethoxy)hydroxyphosphinyl]oxy]-2-hydroxypropyl Ester.*

LHPE [R.N. 85046-18-0]: Spectra: IR,[2252] $^{1}H$ and $^{13}C$ NMR,[2252] $^{31}P$ NMR (fig.),[2308] FAB-MS,[2252] FD-MS,[2122] X-ray.[2308] Chromatography: TLC,[2252] HPLC,[2252] silica column,[2252] CM-cellulose column.[2308]

2-Linoleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (HLPE), 18:2 LPE, $C_{23}H_{44}NO_7P$. *[R-(Z, Z)]-9,12-Octadecadienoic Acid, 2-[[(2-aminoethoxy)hydroxyphosphinyl]oxy]-1-(hydroxymethyl)ethyl Ester.*

HLPE [R.N. 60701-98-6] Spectra: IR, $^{1}H$ NMR, $^{13}C$ NMR, FAB-MS.[2252] Chromatography: TLC, HPLC, silica column.[2252]

1-Linolenoyl-*sn*-glycero-3-phospho-1′-ethanolamine (LnHPE), 18:3 LPE, $C_{23}H_{42}NO_7P$. *[R-(Z,Z,Z)]-9,12,15-Octadecatrienoic Acid, 3-[[(2-aminoethoxy)hydroxyphosphinyl]oxy]-2-hydroxypropyl Ester.*

LnHPE [R.N. 99881-83-1]: Spectra: $^{1}H$ NMR, $^{31}P$ NMR (fig.), X-ray.[2308] Chromatography: TLC, silica column, CM-cellulose column.[2308]

## Synthesis

PHPE may be prepared (a) by phosphorylation of 2-benzyl-1-palmitoyl-*sn*-glycerol with $POCl_3$ followed by reaction with *N*-BOC-ethanolamine,[2240] (b) by acylation of *N*-trityl-*sn*-glycero-3-phosphoethanolamine with palmitic anhydride or *N*-palmitoylimidazole,[2305] or (c) by enzymatic hydrolysis of DPPE with snake venom phospholipase $A_2$.[2309] HPPE may be prepared by condensation of 2-palmitoyl-1-trityl-*sn*-glycero-3-iodohydrin with silver benzyl 2-tritylaminoethyl phosphate.[2297]

SHPE may be prepared by acylation of *N*-trityl-*sn*-glycero-3-phosphoethanolamine with stearic anhydride[2201] or *N*-stearoylimidazole.[2305]

OHPE may be prepared (a) by condensation of 1-oleoyl-*sn*-glycero-3-iodohydrin with silver benzyl 2-phthalimidoethyl phosphate[2307] or (b) by enzymatic hydrolysis of DOPE with snake venom phospholipase $A_2$.[2308] HOPE may be prepared by enzymatic hydrolysis of DOPE with lipase from the mold *R. arrhizus*.[2309]

LHPE may be prepared (a) by migration of the linoleoyl group during the preparation of HLPE from soybean PE in phosphate buffer[2252] or (b) by enzymatic hydrolysis of DLPE with snake venom phospholipase $A_2$.[2308] HLPE may be prepared by enzymatic hydrolysis of soybean PE with lipase from the fungus *M. javanicus*.[2252]

LnHPE may be prepared by enzymatic hydrolysis of DLnPE with snake venom phospholipase $A_2$.[2308]

## Migration

Migration of the linoleoyl group from *sn*-2 to *sn*-1 occurs during the preparation of HLPE from DLPE in phosphate buffer, resulting in a 91:9 mixture of HLPE and LHPE, but this can be prevented by the use of a borate buffer.[2252]

# *N*-Acylphosphatidylethanolamines

## Occurrence

The occurrence of NAPE and NALPE in plants was first reported by Bomstein[1358] in 1965, and subsequently shown to be widespread in plant tissues. The metabolic pathways for the biosynthesis and turnover of these phospholipids are outlined in Fig. 4-2.

## Physical Properties

1,2,*N*-Tripalmitoyl-*sn*-glycero-3-phospho-1′-ethanolamine (*N*-palmitoyl-DPPE), 16:0-16:0/16:0 NAPE, $C_{53}H_{104}NO_9P$. *(R)-Hexadecanoic Acid, 5-Hydroxy-5-oxido-10-oxo-4,6-dioxa-9-aza-5-phosphapentacosane-1,2-diyl Ester*

*N*-Palmitoyl-DPPE [R.N. 57984-41-5]: mp 52-53 °C, $[\alpha]_D^{20}$ +5.37° ($CHCl_3$),[2313] DSC (fig.).[2314] Spectra: IR (fig.),[2315] Raman (fig.),[2315] FTIR (fig.),[2316] ATR-IR (fig.),[2317] $^1$H NMR (fig.),[1361] FAB-MS.[1361] Chromatography: TLC.[2313]

1,*N*-Dipalmitoyl-2-linoleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (*N*-palmitoyl-PLPE), 16:0-16:0/18:2 NAPE, $C_{55}H_{104}NO_9P$. *[R-(Z,Z)]-9,12-Octadecadienoic Acid, [[[Hydroxy[2-[(1-oxohexadecyl)amino]ethoxy]phosphinyl]oxy]methyl]-2-[(1-oxohexadecyl)oxy]ethyl Ester.*

*N*-Palmitoyl-PLPE [R.N. 168434-64-8]: FAB-MS, CAD-MS/MS.[2311]

2,*N*-Dilinoleoyl-1-palmitoyl-*sn*-glycero-3-phospho-1′-ethanolamine (*N*-linoleoyl-PLPE), 18:2-16:0/18:2 NAPE, $C_{57}H_{104}NO_9P$. *[R-(all Z)]-9,12-Octadecadienoic Acid, Ester with 1,2,3-Propanetriol Monohexadecanoate 1-[2-[(1-oxo-9,12-octadecadienyl)amino]ethyl Hydrogen Phosphate].*

*N*-Linoleoyl-PLPE [R.N. 168434-66-0]: FAB-MS, CAD-MS/MS.[2311]

1,2-Dilinoleoyl-*N*-palmitoyl-*sn*-glycero-3-phospho-1′-ethanolamine (*N*-palmitoyl-DLPE), 16:0-18:2/18:2 NAPE, $C_{57}H_{104}NO_9P$. *[R-(all Z)]-9,12-Octadecadienoic Acid, 1-(3-Hydroxy-3-oxido-8-oxo-2,4-dioxa-7-aza-3-phosphatricos-1-yl)-1,2-ethanediyl Ester.*

*N*-Palmitoyl-DLPE [R.N. 168294-52-8]: FAB-MS, CAD-MS/MS.[2311]

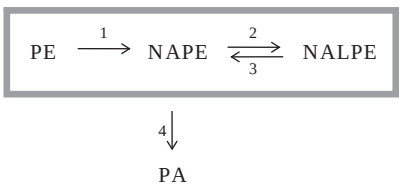



**FIGURE 4-2 Metabolism of *N*-Acyl Phospholipids in Plants**. (1) PE *N*-acyltransferase, fatty acid.[1361] (2) Phospholipase $A_2$.[2310] (3) Fatty acid, Ca(II).[2310] (4) Phospholipase D.[2310]

**Table 4-10** Molecular Species Composition: *N*-Acylphosphatidylethanolamines (mol%)

| No. | Plant part | Method | 16:0 16:0 | 16:0 18:1 | 16:0 18:2 | 16:0 18:3 | 18:0 18:1 | 18:0 18:2 | 18:0 18:3 | 18:1 18:1 | 18:1 18:2 | 18:1 18:3 | 18:2 18:2 | 18:2 18:3 | 18:3 18:3 | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Glycine max* (L.) Merr. (Soybean) | | | | | | | | | | | | | | | | |
| 1 | Seed[a] | HPLC | 0.7 | 7.8[b] | 37.8 | 7.5 | 0.5 | | 1.3 | 0.5 | 6.0 | 2.0 | 25.8 | 8.1 | 2.0 | 1693 |
| *Gossypium hirsutum* L (Upland Cotton) | | | | | | | | | | | | | | | | |
| 1 | Seed[c] | | | | +++ | | | | | | | | | + | | 2311 |
| *Phaseolus coccineus* L. (Scarlet Runner Bean) | | | | | | | | | | | | | | | | |
| 1 | Seed[a] | HPLC | 0.9 | 10.2[b] | 37.9 | 20.8 | 0.5 | | 0.3 | 1.5 | 6.0 | 3.1 | 8.5 | 7.8 | 2.5 | 1693 |
| *Phaseolus vulgaris* L. (Kidney Bean) | | | | | | | | | | | | | | | | |
| 1 | Seed[a] | HPLC | 1.2 | 12.1[b] | 27.6 | 24.9 | 0.5 | | 0.2 | 1.8 | 6.9 | 5.3 | 6.0 | 8.9 | 4.5 | 1693 |
| *Pisum sativum* L. (Pea) | | | | | | | | | | | | | | | | |
| 1 | Seed[d] | AgTLC | 0.4 | 24.7 | 25.3 | | 5.9 | | | 16.1 | 13.9 | | 13.2 | (16:0/18:0, 0.4) | | 2312 |
| 1 | Seed[a] | HPLC | 0.4 | 17.0[b] | 23.9 | 4.1 | 2.6 | | 0.6 | 6.9 | 19.2 | 1.7 | 17.9 | 3.4 | 2.5 | 1693 |
| *Triticum aestivum* L. (Wheat) | | | | | | | | | | | | | | | | |
| 1 | Flour[e] | HPLC | | 11.11 | 23.84 | 3.10 | 12.41 | | | 2.01 | 6.53 | Trace | 22.06 | 1.28 | | 2021 |
| *Vicia faba* L. (Broad Bean) | | | | | | | | | | | | | | | | |
| 1 | Seed[a] | HPLC | 1.0 | 14.9[b] | 26.5 | 1.7 | 2.8 | | 1.2 | 7.7 | 19.8 | 0.9 | 18.8 | 2.3 | 2.3 | 1693 |
| *Vigna angularis* (Willd.) Ohwi and Ohashi (Adzuki Bean) | | | | | | | | | | | | | | | | |
| 1 | Seed[a] | HPLC | 1.0 | 4.3[b] | 37.8[f] | 13.2 | 0.7 | | | 1.2 | 4.8 | 22.6[g] | | 12.4 | 2.0 | 1693 |

[a]N-Acyl group not identified.
[b]Including 18:0/18:2 (SL).
[c]*N*-Acyl mainly 16:0 or 18:2.
[d]*N*-Acyl mainly 16:0, 18:1, or 18:2.
[e]*N*-Acyl mainly 18:2.
[f]Including 18:3/18:0 (LnS).
[g]Including 18:2/18:2 (LL).

### Molecular Species Composition

The molecular species composition of *N*-acylphosphatidylethanolamine in plants, determined by any of the methods described on pages 168–171, is given in Table 4-10.

### Synthesis

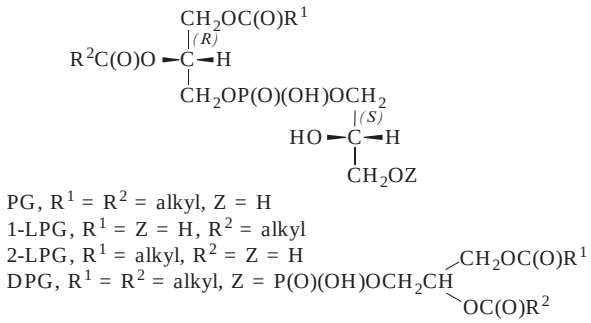
*N*-Palmitoyl-DPPE may be prepared by acylation of DPPE with palmitic anhydride in pyridine.[2313]. No synthesis of any of the other NAPEs has been reported.

### Hydrolysis

Hydrolysis or methanolysis of DL-1,2,*N*-tripalmitoyl NAPE at room temperature converts it not only to the expected deacylation product, DL-glycerol 1-(2-palmitoylaminoethyl hydrogen phosphate), but also, in 20% or higher yield, to *N*-(2-hydroxyethyl)palmitamide. Subsequent heating in aqueous solution at pH 1 cleaves all of the product to *N*-(2-hydroxyethyl)palmitamide.[2318]

## PHOSPHATIDYLGLYCEROLS

This group comprises the phosphatidylglycerols (PG), two kinds of lysophosphatidylglycerols (LPG), and the diphosphatidylglycerols (DPG):




## Phosphatidylglycerols

### Nomenclature

Phosphatidylglycerols containing acyl groups other than *palmitoyl* are named in the IUB system by substituting stearoyl, oleoyl, linoleoyl, linolenoyl, or 3-*trans*-hexadecanoyl for *palmitoyl* and in the Chemical Abstracts system by substituting octadecyl, 9-octadecenyl, 9,12-octadecadienyl, 9,12,15-octadecatrienyl, or 3-hexadecenyl for *hexadecyl* and the prefix [*R*-(*R**,-*S**)], [*R*-[(*R**,*S**-(*Z*))]], [*R*-[(*R**,*S**-(*Z*,*Z*))]], [*R*-[(*R**,*S**-(*Z*,*Z*,*Z*))]], or [*R*-[*R**,*S**-(*E*)]], respectively, for [*R*-(*R**,*S**)]. Chemical Abstracts Registry Numbers are given for each of the phosphatidylglycerols in the following paragraphs.

*Caution*: The numbering of the glycerol carbon atoms in the two systems is different and the naming and numbering of isomer pairs such as 18:0/18:3 and 18:3/18:0 in Chemical Abstracts is also different.

## Stereochemistry

Because both of the glyceryl moieties are asymmetric, PG has two chiral centers—the central carbon atom of each moiety—there are four possible configurations: [*R*,*R*], [*R*,*S*], [*S*,*R*], and [*S*,*S*]. The configuration in the molecular formula illustrated above, [*R*,*S*], is the natural configuration of cabbage leaf and soybean PG[1385] and may well be the natural configuration of all plant PGs. Egg yolk PG, by contrast, contains a 45:55 mixture of [*R*,*S*] and [*R*,*R*] isomers, and *E. coli* PG contains an 89:11 mixture of [*R*,*S*] and [*R*,*R*] isomers.[1385] The orientation of the H and OH atoms in the 1′-glycerol moiety (the lower one in the formula illustrated above) is reversed in the [*R*,*R*] isomer. To date, there are no natural PGs in which the orientation of the other (upper) glycerol moiety is *S*, i.e., [*S*,*R*] or [*S*,*S*].

The absolute stereochemical configuration of PG is not easily determined. Optical rotation alone is inadequate, and enzymic methods based on phospholipases A, C, and D are not absolutely specific except for phospholipase $A_2$. More rigorous methods are required, such as chemical degradation,[1203] chiral phase HPLC,[1385] or synthetic methods employing reagents of known stereochemistry.

In DPG, there is only one chiral center if the acyl substituents are identical, in which case there are only two possible configurations—R and S—and the plant DPGs should contain only the R isomer.

## Occurrence

The principal phosphatidylglycerols of plant tissues are listed below under *Physical Properties*. Those whose molecular species distribution is known are listed in Table 4-11. The phosphatidylglycerols differ from all the other phospholipids (PC, PE, PI, PA, and PS) in two respects.

- Many of them contain high proportions of the rare acid *trans*-3-hexadecenoic acid, located exclusively at the 2-position of the 1-glyceryl moiety (upper one in the formula given above). Roughly half of the PG comprises molecular species in which the $C_2$ substituent is *trans*-3-hexadecenoyl and the $C_1$ substituent is palmitoyl (16:0), stearoyl (18:0), oleoyl (18:1), linoleoyl (18:2), or linolenoyl (18:3). Surveys have shown that PG containing *trans*-3-hexadecenoic acid is characteristic of photosynthetic plant tissue but is not present in etiolated or nonphotosynthetic tissue, or in the PG component of blue-green algae or photosynthetic bacteria.[1348]
- The relative *sn-1* / *sn-2* position of the acyl substituents in the PG tends to have the reverse of the usual order of the phospholipids, e.g. 18:2/16:0 rather than 16:0/18:2.

A few of the molecular species of PG reported in Table 4-11 contain no *trans*-3-hexadecenoyl substituents and their profiles resemble those of the other phospholipids. They are reported separately on the last page of the table under the regular headings.

## Physical Properties

1,2-Dipalmitoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (DPPG), 16:0/16:0 PG. *[R-(R*,S*)]-Hexadecanoic Acid, 1-[[[(2,3-Dihydroxypropoxy)hydroxyphosphinyl]oxy]methyl]-1,2-ethanediyl Ester.*

DPPG [R.N. 74300-16-6]: Homogeneous solid.[2285] Spectra: $^{1}$H NMR,[2285] $^{2}$H and $^{31}$P NMR (figs.).[2321] Chromatography: TLC,[2285] HPLC.[2064] *Na salt* (1:1) [R.N. 74300-11-1]: $[\alpha]_{546}^{30}$ +7.6° ($CHCl_3$/MeOH).[2321] *DPPG* (*R,S* unspecified) [R.N. 4537-77-3]: p$K_a$ 2.9,[2322] DSC.[2177] Spectra: FTIR,[2323] FAB-MS,[2200] FD-MS,[2177] FAB MS/MS (fig.),[2136] fluorescence polarization (fig.).[1631] Chromatography: HPTLC.[1405] Electrophoresis: CE.[2324] *Na salt* (1:1) [R.N. 67232-81-9]: DSC,[2325] LSI-MS.[2239] *R,R-DPPG* [R.N. 74313-95-4]: $[\alpha]_D^{20}$ +6.93° ($CHCl_3$/MeOH 2:1). Spectra: $^{13}$C and $^{31}$P NMR.[2210] *R,rac-DPPG* [R.N. 220407-65-8]: Oil, $[\alpha]_D^{20}$ +6.1° ($CHCl_3$/MeOH 2:1).[2326] Spectra: IR.[2326] Chromatography: TLC,[2326] chiral phase HPLC,[1385] SFC.[2156] Ba salt (2:1) [R.N. 91859-08-4]: Crystals, mp 145-146 °C, $[\alpha]_D^{20}$ +9.0° (pyridine).[2326]

1-Palmitoyl-2-*trans*-3-hexadecenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (P(3t)PG), 16:0/16:1 PG, $C_{38}H_{73}O_{10}P$. *[R-[R*,S*-(E)]]-3-Hexadecenoic Acid, 1-[[[(2,3-Dihydroxypropoxy)hydroxyphosphinyl]oxy]methyl]-2-[(1-oxohexadecyl)oxy]-ethyl Ester.*

P(3t)PG [R.N. 85967-07-3]: Chromatography: HPLC.[2064]

1-Stearoyl-2-palmitoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (SPPG), 18:0/16:0 PG, $C_{40}H_{75}O_{10}P$. *[R-[R*,S*]]-Octadecanoic Acid, 1-[[[(2,3-Dihydroxypropoxy)hydroxyphosphinyl]oxy]methyl]-2-[(1-oxohexadecyl)oxy]ethyl Ester.*

SPPG [R.N. 132922-64-6]: Chromatography: HPLC.[1594]

1-Stearoyl-2-*trans*-3-hexadecenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (S(3t)PG), 18:0/16:1 PG, $C_{40}H_{73}O_{10}P$. *[R-[R*,S*-(E)]]-Octadecanoic Acid, 3-[[(2,3-Dihydroxypropoxy)hydroxyphosphinyl]oxy]2-[(1-oxo-3-hexadecenyl)oxy]propyl Ester.*

S(3t)PG [R.N. 132943-54-5]: Chromatography: HPLC.[2064]

1-Oleoyl-2-palmitoylphosphatidylglycerol (OPPG), 18:1/16:0 PG, $C_{40}H_{77}O_{10}P$. *[R-[R*,S*-(Z)]]-9-Octadecenoic Acid, Monoester with 1,2,3-Propanetriol 1,1′-(Hydrogen phosphate) Monohexadecanoate*

OPPG [R.N. 134623-65-7]: Chromatography: HPLC.[1892] *OPPG* (*R,S* unspecified) [R.N. 81490-05-3]: Electrophoresis: CE (fig.).[2181] Na salt (1:1): White powder, mp 176-179 °C, $[\alpha]_D^{20}$ +1.02° ($CHCl_3$)[2327]; IR.[2327] Chromatography: PC, TLC, silica gel column.[2327]

1-Oleoyl-2-*trans*-3-hexadecenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol O(3t)PG, 18:1/16:1 PG, $C_{40}H_{75}O_{10}P$. *[R-[R*,S*-(E,Z)]]-9-Octadecenoic Acid, 3-[[(2,3-Dihydroxypropoxy)hydroxyphosphinyl]oxy]-2-[(1-oxo-3-hexadecenyl)oxy]propyl Ester.*

O(3t)PG [R.N. 132922-63-5]: Chromatography: HPLC.[1594]

1,2-Dioleoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (DOPG), 18:1/18:1 PG, $C_{42}H_{79}O_{10}P$. *[R-[R*,S*-(Z)]]-9-Octadecenoic Acid, 1-[[[(2,3-Dihydroxypropoxy)hydroxyphosphinyl]oxy]-methyl]-1,2-ethanediyl Ester*

**Table 4-11** Molecular Species Composition: Phosphatidylglycerols (mol%)

| No. | Plant part | | 16:0 16:0 | 18:0 16:0 | 18:1 16:0 | 18:2 16:0 | 18:3 16:0 | 16:0 16:1 | 18:0 16:1 | 18:1 16:1 | 18:2 16:1 | 18:3 16:1 | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Allium fistulosum* L. (Welsh Onion) | | | | | | | | | | | | | |
| 1 | Leaf | GLC | 5 | 1 | 4 | 27 | 26 | 2 | 0 | 1 | 11 | 24 | 2112 |
| *Aquilegia alpina* L. (Alpine Columbine) | | | | | | | | | | | | | |
| 1 | Leaf | HPLC | | | 3.2 | 16.3 | 10.5 | | | | 25.8 | 42.6 | 2109 |
| *Arabidopsis thaliana* (L.) Heynh (Mouse-Ear Cress) | | | | | | | | | | | | | |
| 1 | Leaf | HPLC | 3.5 | | 7.2 | 11.7 | 19.9 | 4.8 | 0.5 | 2.3 | 6.2 | 43.3 | 2319 |
| *Avena sativa* L. (Oats) | | | | | | | | | | | | | |
| 1 | Leaf | GLC | 3 | 0 | 2 | 11 | 33 | 2 | 0 | 0 | 3 | 45 | 2112 |
| *Avicennia germinans* (L.) L. (Black Mangrove) | | | | | | | | | | | | | |
| 2 | Chilling-tolerant, leaf | GLC | 41.6[a] | Trace | 40.9[b] | 6.2 | 4.8 | | 2.8 | | 3.7 | Trace | 2138 |
| | –, root | GLC | 34.8[a] | 9.0 | 12.8 | 10.1 | 2.2 | | | | 2.3 | 2.6 | 2138 |
| | Chilling-sensitive, leaf | GLC | 49.2[a] | Trace | 31.7[b] | 6.4 | 5.2 | | 2.3 | | 5.2 | Trace | 2138 |
| | –, root | GLC | 21.3[a] | 4.2 | 18.6 | 24.5 | 7.9 | | | | Trace | 2.5 | 2138 |
| *Brassica campestris* L. ssp. *komatsuma* Mak. (Chinese Cabbage) | | | | | | | | | | | | | |
| 1 | Leaf | GLC | 4 | 1 | 2 | 9 | 47 | 3 | 0 | 0 | 3 | 32 | 2112 |
| *Brassica napus* L. (Rape, low erucic acid (Canola)) | | | | | | | | | | | | | |
| 1 | Leaf | HPLC | | | 2.0 | 21.0 | 53.0 | | | | 4.0 | 20.0 | 2117 |
| *Brassica oleracea* L. ssp. *capitata* L. (Cabbage) | | | | | | | | | | | | | |
| 1 | Leaf | GLC | 3 | 0 | 4 | 45 | 43 | 1 | 0 | 0 | 2 | 2 | 2112 |
| *Citrus amblycarpa* (Hassk.) Ochse (Djeroek Limoe) | | | | | | | | | | | | | |
| 1 | Leaf | HPLC | 4 | 1 | 20 | 1[c] | 3 | 10 | 4 | 46 | 5 | 7 | 1594 |
| *Citrus grandis* (L.) Osbeck (Tosa-Buntan) | | | | | | | | | | | | | |
| 1 | Leaf | HPLC | 6 | 1 | 11 | 6[c] | 3 | 22 | 3 | 26 | 9 | 10 | 1594 |
| *Citrus junos* (Sieb.) Tanaka (Yuzu) | | | | | | | | | | | | | |
| 1 | Leaf | HPLC | 4 | 1 | 17 | 1[c] | 1 | 14 | 6 | 43 | 5 | 6 | 1594 |
| *Citrus* × *paradisi* Macf. (Pomelo) | | | | | | | | | | | | | |
| 1 | Leaf | HPLC | 7 | 1 | 34 | 2[c] | 2 | 11 | 2 | 32 | 4 | 4 | 1594 |
| *Citrus sinensis* (L.) Osbeck (Orange) | | | | | | | | | | | | | |
| 2 | Leaf (1) | HPLC | 9 | 1 | 23 | 3[c] | 2 | 11 | 3 | 36 | 5 | 3 | 1594 |
| | Leaf (2) | HPLC | 4 | 1 | 21 | 1[c] | 1 | 11 | 4 | 47 | 5 | 4 | 1594 |
| *Citrus unshiu* Marc. (Mandarin) | | | | | | | | | | | | | |
| 1 | Leaf | HPLC | 9 | 3 | 35 | 3[c] | 2 | 10 | 4 | 29 | 2 | 3 | 1594 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Colocasia esculenta* (L.) Schott (Taro) | | | | | | | | | | | | |
| 1 | Leaf | GLC | 20 | 1 | 3 | 11 | 7 | 42 | 3 | 3 | 4 | 6 | 2112 |
| *Cucumis sativus* L. (Cucumber) | | | | | | | | | | | | |
| 1 | Leaf | HPLC | 22.0 | 14.0 | 26.0 | 4.0 | 5.0 | 23.4 | | | 2.1 | 3.5 | 2104 |
| *Cucurbita moschata* Duch. (Warty Squash) | | | | | | | | | | | | |
| 1 | Leaf | GLC | 17 | 0 | 0 | 13 | 23 | 24 | 2 | 5 | 3 | 23 | 2112 |
| *Cyclamen persicum* Mill. (Cyclamen) | | | | | | | | | | | | |
| 1 | Leaf | GLC | 5 | 0 | 11 | 8 | 4 | 21 | 3 | 34 | 8 | 5 | 2112 |
| *Gossypium hirsutum* L. (Upland Cotton) | | | | | | | | | | | | |
| 1 | Leaf | HPLC | 33.4 | 7.4 | 13.1 | 3.5 | 5.0 | 26.5 | | | 5.6 | 5.6 | 2104 |
| *Ipomoea batatas* (L.) Lam. (Sweet Potato) | | | | | | | | | | | | |
| 1 | Leaf | GLC | 26 | 3 | 7 | 4 | 2 | 39 | 3 | 8 | 4 | 4 | 2112 |
| *Kalanchoë daigremontiana* Ham. and Perr. (Devil's Backbone) | | | | | | | | | | | | |
| 1 | Leaf | GLC | 32 | 3 | 19 | 26 | 11 | 2 | 0 | 0 | 1 | 6 | 2112 |
| *Lactuca sativa* L. (Lettuce) | | | | | | | | | | | | |
| 1 | Leaf | GLC | 13 | 0 | 1 | 26 | 26 | 4 | 1 | 1 | 4 | 24 | 2112 |
| *Luffa aegyptiaca* Mill. (Sponge Gourd) | | | | | | | | | | | | |
| 1 | Leaf | GLC | 16 | 2 | 4 | 5 | 4 | 23 | 13 | 19 | 3 | 11 | 2112 |
| *Lycoris radiata* Herb. (Red Spiderlily) | | | | | | | | | | | | |
| 1 | Leaf | GLC | 6 | 0 | 6 | 28 | 23 | 5 | 2 | 3 | 7 | 20 | 2112 |
| *Nerium oleander* L. (Oleander) | | | | | | | | | | | | |
| 1 | Leaf, thylakoid | HPLC | 2.6 | 0.7 | 21.4 | 13.0 | 2.2 | 4.6 | Trace | 50.8 | 7.9 | 2.2 | 1814 |
| *Nicotiana tabacum* L. (Tobacco) | | | | | | | | | | | | |
| 1 | Leaf | GLC | 19 | 0 | 1 | 11 | 7 | 20 | 5 | 15 | 7 | 16 | 2112 |
| 1 | Leaf | HPLC | | | | 17.3 | 11.6 | | | | 21.9 | 49.1 | 1410 |
| *Oriza sativa* L. (Rice) | | | | | | | | | | | | |
| 2 | Leaf thylakoid, chilling-resistant | GLC | 13.3 | | 9.8 | 9.6 | 5.9 | 38.7 | 1.4 | | 13.4 | 7.9 | 2320 |
| | Leaf thylakoid, chilling-sensitive | GLC | 33.7 | 0.6 | 10.2 | 1.8 | 0.8 | 42.1 | 2.7 | 4.3 | 1.2 | 17.2 | 2320 |
| | | Data also given for 15 other varieties having intermediate levels of chilling resistance | | | | | | | | | | | 2320 |

[a]Including about 10-15% of 16:0/16:1 PG; [b]Including 18:1/16:1 PG; [c]Including 16:0/18:3 (PLn); [d]Including 18:3/18:0 (LnS); [e]Including 18:0/18:2 (SL); [f]Including 14:0/18:0; [g]Including 18:2/18:2 (LL).

*Continued*

**Table 4-11** Molecular Species Composition: Phosphatidylglycerols (mol%)—cont'd

| No. | Plant part | | 16:0 16:0 | 18:0 16:0 | 18:1 16:0 | 18:2 16:0 | 18:3 16:0 | 16:0 16:1 | 18:0 16:1 | 18:1 16:1 | 18:2 16:1 | 18:3 16:1 | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pinus nigra* Arnold (Black Pine) | | | | | | | | | | | | | |
| 1 | Needle (leaf) | HPLC | 4 | | <1 | 36 | (18:1/18:3, 13) | | 3 | | 13[b] | 18 | 1892 |
| *Pisum sativum* L. (Pea) | | | | | | | | | | | | | |
| 1 | Leaf | GLC | 12 | 1 | 27 | 15 | 15 | 7 | 0 | 6 | 10 | 7 | 2112 |
| 1 | Leaf chloroplast | HPLC | | 1 | 15 | 22 | 28 | | | | 5 | 28 | 1909 |
| 1 | Leaf mitochondria | HPLC | | | 9 | 36 | 38[d] | | | | | | 1909 |
| *Raphanus acanthiformis* Backer (Japanese Radish) | | | | | | | | | | | | | |
| 1 | Leaf | GLC | 5 | 1 | 3 | 5 | 51 | 3 | 0 | 1 | 4 | 26 | 2112 |
| *Raphanus sativus* L. (Radish) | | | | | | | | | | | | | |
| 1 | Seedling | HPLC | 2.8 | | 6.2 | 19.8 | 58.9 | 0.1 | | | | 1.6 | 2131 |
| *Ricinus communis* L. (Castor Bean) | | | | | | | | | | | | | |
| 1 | Leaf | GLC | 20 | 7 | 15 | 3 | 1 | 22 | 1 | 29 | 1 | 1 | 2112 |
| *Spinacea oleracea* L. (Spinach) | | | | | | | | | | | | | |
| 1 | Leaf | AgTLC | | | | 2 | 9 | 7 | (16:0/18:3, 12) | | | 56 | 2095 |
| 1 | Leaf | GLC | 1 | 0 | 1 | 5 | 16 | 5 | 0 | 0 | 0 | 72 | 2112 |
| 1 | Leaf, chloroplast envelope | GC-MS | | | | | + | | | | | +++ | 2141 |
| *Taraxacum* spp. (Dandelion) | | | | | | | | | | | | | |
| 1 | Leaf | GLC | 2 | 0 | 3 | 16 | 15 | 2 | 0 | 12 | 29 | 20 | 2112 |
| *Trifolium pratense* L. (Red Clover) | | | | | | | | | | | | | |
| 1 | Leaf | GLC | 4 | 0 | 5 | 11 | 12 | 6 | 0 | 23 | 14 | 25 | 2112 |
| *Triticum aestivum* L. (Wheat) | | | | | | | | | | | | | |
| 1 | Leaf | GLC | 1 | 0 | 2 | 11 | 32 | 2 | 0 | 0 | 5 | 47 | 2112 |
| *Vigna unguiculata* (L.) Walp. (Cowpea) | | | | | | | | | | | | | |
| 2 | Leaf, drought-resistant | HPLC | 12 | | 5 | | 8 | 39 | 10 | | 5 | 19 | 2064 |
| | Leaf, drought-sensitive | HPLC | 11 | | 6 | | 14 | 53 | | | | 16 | 2064 |
| *Zea mays* L. (Corn) | | | | | | | | | | | | | |
| 1 | Leaf | GLC | 20 | 0 | 0 | 5 | 17 | 17 | 0 | 4 | 11 | 26 | 2112 |

| No. | Plant part | Method | 16:0 16:0 | 16:0 18:1 | 16:0 18:2 | 16:0 18:3 | 18:0 18:1 | 18:0 18:2 | 18:0 18:3 | 18:1 18:1 | 18:1 18:2 | 18:1 18:3 | 18:2 18:2 | 18:2 18:3 | 18:3 18:3 | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | *Note changed table headings* | | | | | | | | |
| *Daucus carota* L. (Carrot) | | | | | | | | | | | | | | | | |
| 1 | Cell culture | AgTLC | | 7.2 | 59.1 | | | | | | 5.5 | | 19.3 | 8.9 | | 1648 |
| *Dianthus caryophyllus* L. (Carnation) | | | | | | | | | | | | | | | | |
| 1 | Flower microsomal membr. | GLC | 17.6 | 10.2 | 64.6 | 7.3 | | (16:0/18:0, 0.2) | | | | | | | | 1652 |
| *Glycine max* (L.) Merr. (Soybean) | | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | 2.9 | 14.1[e] | 52.2 | 7.3 | 0.8 | | 1.8 | 2.4 | 5.3 | 0.9 | 9.7 | 2.0 | 0.6 | 1693 |
| *Phaseolus coccineus* L. (Scarlet Runner Bean) | | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | 7.5 | 13.9[e] | 47.2 | 20.7 | 0.9 | | 0.4 | 0.5 | 2.4 | 1.2 | 2.7 | 1.8 | 0.8 | 1693 |
| *Phaseolus vulgaris* L. (Kidney Bean) | | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | 3.5 | 13.1[e] | 30.9 | 34.5 | 0.6 | | 2.5 | 1.1 | 2.2 | 2.6 | 2.9 | 3.6 | 2.6 | 1693 |
| *Pisum sativum* L. (Pea) | | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | 20.1 | 24.6[e] | 37.3 | 4.2 | 0.7 | | 4.0 | 0.6 | 2.0 | 3.4 | 2.2 | 0.5 | 0.3 | 1693 |
| *Secale cereale* L. (Rye) | | | | | | | | | | | | | | | | |
| 1 | Leaf plasma membrane | GLC | 5.0[f] | 5.1 | 47.6 | 28.1 | | | | | | Trace[g] | | Trace | | 1962 |
| *Vicia faba* L. (Broad Bean) | | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | 15.3 | 23.6[e] | 50.4 | 1.2 | 1.0 | | 0.2 | 0.8 | 3.4 | 0.2 | 2.9 | 0.4 | 0.5 | 1693 |
| *Vigna angularis* (Willd.) Ohwi and Ohashi (Adzuki Bean) | | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | 18.4 | 7.8 [e] | 47.0 | 12.5 | | | 0.5 | | 2.5 | 1.2 | 4.8 | 3.8 | 1.6 | 1693 |
| 1 | Cell culture, cotyledon | HPLC | Trace | 11[e] | 16 | 21 | | | 13 | | | | 3 | 7 | | 2052 |
| 1 | –, leaf | HPLC | Trace | 8[e] | 21 | 26 | | | 9 | | | | 6 | 9 | | 2052 |
| 1 | –, hypocotyl | HPLC | Trace | 10[e] | 15 | 29 | | | 8 | | | | 8 | 8 | | 2052 |

[a]Including about 10-15% of 16:0/16:1 PG.
[b]Including 18:1/16:1 PG.
[c]Including 16:0/18:3 (PLn).
[d]Including 18:3/18:0 (LnS).
[e]Including 18:0/18:2 (SL).
[f]Including 14:0/18:0.
[g]Including 18:2/18:2 (LL).

DOPG [R.N. 109009-74-7]: DSC.[2328] *DOPG* (*R,S* unspecified) [R.N. 62700-69-0]: Spectra: $^{1}H$ and $^{13}C$ NMR,[2329] $^{31}P$ NMR (fig.).[2286] Chromatography: TLC,[2166] HPLC.[2251] Na salt (1:1): Spectra: FAB-MS,[2329] LSI-MS.[2239] *R,rac DOPG*: Spectra: MS (fig.).[1385] Chromatography: Chiral phase HPLC.[1385]

1-Linoleoyl-2-palmitoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (LPPG), 18:2/16:0 PG, $C_{40}H_{75}O_{10}P$. *[R-[R*,S*-(Z,Z)]]-9,12-Octadecadienoic Acid, 3-[[(2,3-Dihydroxypropoxy)-hydroxyphosphinyl]oxy]-2-[(1-oxohexadecyl)oxy]propyl Ester.*
LPPG [R.N. 120444-75-9]: Chromatography: HPLC.[1410]

1-Linoleoyl-2-*trans*-3-hexadecenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (L(3t)PG), 18:2/16:1 PG, $C_{40}H_{73}O_{10}P$. *[R-[R*,S*-(E,Z,Z)]]-9,12-Octadecadienoic Acid, 3-[[(2,3-Dihydroxypropoxy)-hydroxyphosphinyl]oxy]-2-[(1-oxo-3-hexadecenyl)oxy]propyl Ester.*
L(3t)PG [R.N. 120407-77-4]: Chromatography: HPLC.[1410,2104]

1,2-Dilinoleoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (DLPG), 18:2/18:2 PG, $C_{42}H_{75}O_{10}P$. *[R-[(R*,S*-(all Z)]]-9,12-Octadecadienoic Acid, 1-[[[(2,3-Dihydroxypropoxy) hydroxyphosphinyl]-oxy]methyl]-1,2-ethanediyl Ester.*
DLPG [R.N. 120851-76-5]: Chromatography: HPLC.[2064] *R,rac-DLPG*: Chiral phase HPLC.[1385]

1-Linolenoyl-2-palmitoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (LnPPG), 18:3/16:0 PG, $C_{40}H_{73}O_{10}P$. *[R-[R*,S*-(Z,Z,Z)]]-9,12,15-Octadecatrienoic Acid, 3-[[(2,3-Dihydroxypropoxy)-hydroxyphosphinyl]oxy]-2-[(1-oxohexadecyl)oxy]propyl Ester.*
LnPPG [R.N. 120407-76-3]: Chromatography: HPLC.[2109]

1-Linolenoyl-2-*trans*-3-hexadecenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (Ln(3t)PG), 18:3/16:1 PG, $C_{40}H_{71}O_{10}P$. *[R-[R*,S*-(E,Z,Z,Z)]]-9,12,15-Octadecatrienoic Acid, 3-[[(2,3-Dihydroxypropoxy)-hydroxyphosphinyl]oxy]-2-[(1-oxo-3-hexadecenyl)oxy]propyl Ester.*
Ln(3t)PG [R.N. 120444-76-0]: Chromatography: HPLC.[1410,2104]

1,2-Dilinolenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (DLnPG), 18:3/18:3 PG, $C_{42}H_{71}O_{10}P$. *[R-[R*,S*-(all Z)]]-9,12,15-Octadecatrienoic Acid, 1-[[[(2,3-Dihydroxypropoxy) hydroxyphosphinyl]oxy]methyl]-1,2-ethanediyl Ester.*
DLnPG [R.N. 132922-60-2]: Chromatography: HPLC.[1594]

## Molecular Species Composition

The molecular species composition of phosphatidylglycerol in plants, determined by any of the methods described on pages 168–171, is given in Table 4-11.

## Synthesis

DPPG may be prepared (a) by phosphorylation of 1,2-dipalmitoyl-*sn*-glycerol with $POCl_3$ followed by reaction with 2,3-dibenzyl-*sn*-glycerol,[2217] (b) by condensation of DPPA[2321] or its mono(2,2,2-trichloroethyl) ester[2285] with 2,3-isopropylidene-*sn*-glycerol

or 2,3-dibenzyl-*sn*-glycerol, respectively, in the presence of mesitylenesulfonyl chloride, or (c) by enzymatic transesterification of DPPC with glycerol in the presence of phospholipase D.[2330] OPPG may be prepared by the reaction of silver benzyl 2,3-isopropylidene-*sn*-glycero-1-phosphate with 1-oleoyl-2-palmitoyl-*sn*-glycero-3-iodohydrin.[2327] DOPG may be prepared by transesterification of DPPC with glycerol in the presence of phospholipase D.[2260,2329]

### Hydrolysis

The hydrolysis of DPPG in acetate buffer (pH 4.0, 30 °C) proceeds at a faster rate than DPPC or DPPE ($k_{obs.} = 17 \times 10^{-2}$, $1.0 \times 10^{-2}$ and $0.7 \times 10^{-2}$ days$^{-1}$, respectively), but the rates are not significantly different if corrections are made for surface charge effects.[2228]

## Lysophosphatidylglycerols

### Physical Properties

1-Palmitoyl-*sn*-glycero-3-phospho-*sn*-1′-glycerol (PHPG), 16:0 PG, $C_{22}H_{45}O_9P$. *[R-(R*, R*)]-Hexadecanoic Acid, 3-[[(2,3-dihydroxypropoxy)hydroxyphosphinyl]oxy]-2-hydroxypropyl Ester.*

PHPG [R.N. 30227-18-0]: Water soluble[2240]; critical micelle concentration.[2235]
Chromatography: TLC.[2240]

1-Stearoyl-*sn*-glycero-3-phospho-*sn*-1′-glycerol (SHPG), 18:0 PG, $C_{24}H_{49}O_9P$. *[R-(R*,R*)]-Octadecanoic Acid, 3-[[(2,3-dihydroxypropoxy)hydroxyphosphinyl]oxy]-2-hydroxypropyl Ester.*

SHPG: Chromatography: TLC.[2240]

1-Oleoyl-*sn*-glycero-3-phospho-*sn*-1′-glycerol (OHPG), 18:1 PG. $C_{24}H_{47}O_9P$. *[R-[R*,R*-(Z)]]-9-Octadecenoic Acid, 3-[[(2,3-dihydroxypropoxy)hydroxyphosphinyl]oxy]-2-hydroxypropyl Ester.*

OHPG [R.N. 125715-20-0]: Solid, soluble in ethanol, insoluble in ether.
Chromatography: TLC.[2331]

### Synthesis

PHPG may be prepared (a) by phosphorylation of 2-benzyl-1-palmitoyl-*sn*-glycerol followed by reaction with 2,3-dibenzyl-*sn*-glycerol[2240] or (b) by enzymatic hydrolysis of DPPG with *Naja naja* snake venom phospholipase $A_2$.[2235] HPPG may be prepared by enzymatic hydrolysis of DPPG with lipase from the mold *R. arrhizus*.[2232] SHPG may be prepared by phosphorylation of 2-benzyl-1-stearoyl-*sn*-glycerol followed by reaction with 2,3-dibenzyl-*sn*-glycerol[2240] OHPG may be prepared by enzymatic hydrolysis of DOPG with *C. adamanteus* snake venom phospholipase $A_2$.[2331]

# Diphosphatidylglycerol

## Physical Properties

1′,3′-bis(1,2-Dipalmitoyl-*sn*-glycero-3-phospho)-*sn*-glycerol (DPDPG), $(16:0/16:0)_2$, $C_{73}H_{142}O_{17}P_2$. *[R-(R*,R*)]-Hexadecanoic Acid, 5,8,11-Trihydroxy-5,11-dioxido-4,6,10,12-tetraoxa-5,11-diphosphapentadecane-1,2,14,15-tetrayl Ester.*

DPDPG [R.N. 105380-95-8]: Oil, $[\alpha]_D^{20}$ +5.1° ($CHCl_3$).[2326] Spectra: IR.[2326] Chromatography: TLC.[2326]

$Na_2C_{73}H_{140}O_{17}P_2.2H_2O$ [R.N. 64043-42-1]: Mp 199-201 °C, $[\alpha]_D^{21}$ +8.50° ($CHCl_3$/MeOH/$H_2O$ 4:4:1),[2332] DSC.[2333] Spectra: IR, $^1$H NMR, $^{31}$P NMR.[2332] Chromatography: TLC.[2332]

$(NH_4)_2C_{73}H_{140}O_{17}P_2{\cdot}2H_2O$ [R.N. 64043-41-0]: Amorphous solid (X-ray), mp 177-178 °C, $[\alpha]_D^{21}$ +9.25° ($CHCl_3$/MeOH/$H_2O$ 4:4:1), $[\alpha]_D^{24}$ +6.35° ($CHCl_3$)[2332]; DSC.[2333] Spectra: IR, $^1$H NMR.[2332] Chromatography: TLC.[2332]

1′,3′-bis(1-Stearoyl-2-oleoyl-*sn*-glycero-3-phospho)-*sn*-glycerol (SODPG), $(18:0/18:1)_2$, $C_{81}H_{154}O_{17}P_2$.

SODPG: Chromatography: PC, TLC.[2334]

1′,3′-bis(1,2-Dioleoyl-*sn*-glycero-3-phospho)-*sn*-glycerol (DODPG), $(18:1/18:1)_2$, $C_{81}H_{150}O_{17}P_2$ *[R-[R*,R*-(Z)]]-9-Octadecenoic Acid, 5,8,11-Trihydroxy-5,11-dioxido-4,6,10,12-tetraoxa-5,11-diphosphapentadecane-1,2,14,15-tetrayl Ester.*

DODPG [R.N. 115405-83-9]: No data. *R,rac* [R.N. 121545-98-0] (prepared by condensing DOPG with DOPA): Spectra: $^{31}$P NMR (fig.) and $^1$H NMR. Chromatography: TLC.[2335]

$Na_2C_{81}H_{152}O_{17}P_2$: Crystals, mp 202-204 °C, $[\alpha]_D^{20}$ +5.81° ($CHCl_3$).[2336]

$BaC_{81}H_{152}O_{17}P_2$: Colorless crystals, mp 192-194 °C, $[\alpha]_D^{20}$ −6.25° ($CHCl_3$).[2336] A comparable difference in optical activity is found between the sodium and barium salts of ox heart cardiolipin.[2336]

1′,3′-bis(1,2-Dilinoleoyl-*sn*-glycero-3-phospho)-*sn*-glycerol (DLDPG), $(18:2/18:2)_2$, $C_{81}H_{142}O_{17}P_2$. *[R-[R*,R*-(Z,Z)]]-9,12-Octadecadienoic Acid, 5,8,11-Trihydroxy-5,11-dioxido-4,6,10,12-tetraoxa-5,11-diphosphapentadecane-1,2,14,15-tetrayl Ester.*

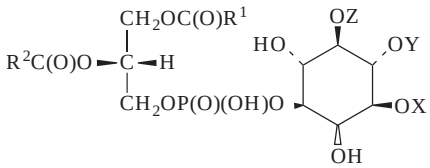
DLDPG [R.N. 152595-52-3]: Spectra: $^2$H and $^{31}$P NMR (figs.),[2337] FAB-MS/MS.[2136] Electrophoresis: CE.[2324]

## Synthesis

DPDPG may be prepared (a) by the reaction of 1,2-dipalmitoyl-*sn*-glycerol with bis(1,2-dimethylethenylene) pyrophosphate and 2-(*t*-butyldimethylsilyl)glycerol in the presence of triethylamine[2332] or (b) by the reaction of DPPA with 2-benzylglycerol in the presence of mesitylenesulfonyl chloride.[2326] Other methods are available that give DPDPGs that are racemic at either one or more of the three glycerol residues.[2326,2338,2339] DODPG may be prepared by condensation of DOPA with 2-(*t*-butyldimethylsilyl)glycerol in the presence of mesitylenesulfonyl chloride.[2340] SODPG may be prepared by the reaction of silver benzyl SOPA with 1,3-diiodo-2-propanol.[2336]

# PHOSPHATIDYLINOSITOLS

This group comprises the phosphatidylinositols (PI), the lysophosphatidylinositols (LPI), and their phosphates (PIP, $PIP_2$, and LPIP). Note that the stereochemical configuration of the phosphatidylinositols is L-α at the glycerol center like the other phospholipids but D at the *myo*-inositol center like the *myo*-inositol phosphates of Chapters 2 and 3:




PI, $R^1 = R^2$ = alkyl
1-LPI, $R^1$ = H, $R^2$ = alkyl
2-LPI, $R^1$ = alkyl, $R^2$ = H
PI(3)P, $R^1 = R^2$ = alkyl, X = $P(O)(OH)_2$, Y = Z = H
PI(4)P, $R^1 = R^2$ = alkyl, Y = $P(O)(OH)_2$, X = Z = H
LPI(4)P, Y = $P(O)(OH)_2$, $R^1$ = X = Z = H, $R^2$ = alkyl
PI(3,4)$P_2$, $R^1 = R^2$ = alkyl, X = Y = $P(O)(OH)_2$, Z = H
PI(4,5)$P_2$, $R^1 = R^2$ = alkyl, Y = Z = $P(O)(OH)_2$, X = H

## Phosphatidylinositols

### Physical Properties

1,2-Dipalmitoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (DPPI), 16:0/16:0 PI, $C_{41}H_{79}O_{13}P$. D-myo-*Inositol, (R)-1-[2,3-bis[(1-oxohexadecyl)oxy]propyl Hydrogen Phosphate]*.

DPPI [R.N. 28366-80-5]: White solid, mp 181 °C dec., $[\alpha]_D^{20}$ +9.3° ($CHCl_3$).[2341] Spectra: IR,[2342] $^1$H NMR,[2341] $^{31}$P NMR,[2343] FAB-MS (fig.).[2342] Chromatography: HPLC.[2101]

$NaC_{41}H_{78}O_{13}P$ [R.N. 154459-87-7]: White solid, mp 214-217 °C. Spectra: $^1$H and $^{31}$P NMR.[2344]

$NH_4C_{41}H_{78}O_{13}P$ [R.N. 34290-57-8]: Precipitate, mp 169-172 °C, $[\alpha]_D^{20}$ +7.48° ($CHCl_3$/methanol), soluble in chloroform and methanol, insoluble in acetone; ORD (fig.), IR (fig.), TLC.[2345]

1-Palmitoyl-2-oleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (POPI), 16:0/18:1 PI, $C_{43}H_{81}O_{13}P$. D-myo-*Inositol, [R-(Z)]-1-[3-[(1-oxohexadecyl)oxy]-2-[(1-oxo-9-octadecenyl)oxy]propyl Hydrogen Phosphate]*.

POPI [R.N. 51547-49-0]: Spectra: FAB-MS (fig.),[2137] CI-MS.[2137] Chromatography: HPLC,[2101] HPLC-MS.[2106]

$NH_4C_{43}H_{80}O_{13}P$ [R.N. 50730-13-7]: White powder, mp 172-174 °C, $[\alpha]_D$ +6.1° ($CHCl_3$), ORD (fig.).[2346]

1-Palmitoyl-2-linoleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (PLPI), 16:0/18:2 PI, $C_{43}H_{79}O_{13}P$. D-myo-*Inositol, [R-(Z,Z)]-1-[3-[(1-oxohexadecyl)oxy]-2-[(1-oxo-9,12-octadecadienyl)oxy]propyl Hydrogen Phosphate]*.

**Table 4-12** Molecular Species Composition: Phosphatidylinositols (mol%)

| No. | Plant part | Method | 16:0 16:0 | 16:0 18:1 | 16:0 18:2 | 16:0 18:3 | 18:0 18:1 | 18:0 18:2 | 18:0 18:3 | 18:1 18:1 | 18:1 18:2 | 18:1 18:3 | 18:2 18:2 | 18:2 18:3 | 18:3 18:3 | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Camellia sinensis* L. (Tea) | | | | | | | | | | | | | | | | |
| 1 | Pollen | HPLC | | | | + | | | | | | | | | + | 1558 |
| *Dianthus caryophyllus* L. (Carnation) | | | | | | | | | | | | | | | | |
| 1 | Flower microsomal membr. | GLC | 3.8 | 9.0 | 56.8 | 2.4 | | 2.9 | (16:0/18:0, 1.9) | | 3.9 | 3.0 | 11.6 | 1.8 | | 1652 |
| *Diptychocarpus strictus* (Fisch.) Trautv. | | | | | | | | | | | | | | | | |
| 1 | Seed | 1R,2R | 1.6 | 5.0 | 14.0 | 40.0 | 0.1 | 0.7 | 1.0 | 1.0 | 2.0 | 6.3 | 1.2 | 3.3 | 4.2 | 959 |
| *Glycine max* (L.) Merr. (Soybean) | | | | | | | | | | | | | | | | |
| 1 | Seed | GLC | 0.1 | 4.3 | 57.3 | 6.8 | 1.0 | 13.1 | 1.3 | 0.3 | 3.6 | | 6.5 | 1.0[a] | | 2114 |
| 1 | Seed | 1R,2R | 4.0 | 4.8 | 50.7 | 5.9 | 1.1 | 11.9 | 1.4 | 0.3 | 2.8 | 0.3 | 5.8 | 0.7 | 0.07 | 2114 |
| 1 | Seed | HPLC | 0.1 | 17.5[b] | 47.1 | 10.6 | 1.0 | | 3.4 | 0.6 | 5.0 | 1.1 | 9.1 | 3.3 | 1.1 | 1693 |
| 1 | –, hypocotyl | AgTLC | | | 57 | 24 | | 8 | | | 1 | | 3 | 1 | Trace | 1690 |
| 1 | –, cotyledon | AgTLC | | | 61 | 9 | | 14 | | | 1 | | 2 | 1 | Trace | 1690 |
| 1 | Seedling, microsomes | HPLC | | 12.7 | 52.7 | 10.7 | Trace | 16.3 | Trace | | 3.3 | | 4.3 | Trace | | 1983 |
| *Gossypium barbadense* L. (Sea Island Cotton) | | | | | | | | | | | | | | | | |
| 1 | Seed kernel | 1R,2R | 8.3 | 13.1 | 53.0 | | 1.2 | 5.0 | | 0.5 | 2.0 | | 1.8 | | | 1709 |
| *Gossypium hirsutum* L. (Upland Cotton) | | | | | | | | | | | | | | | | |
| 1 | Seed kernel | 1R,2R | 3.2 | 4.8 | 39.9 | | 0.9 | 7.2 | | 1.0 | 8.4 | | 13.2 | | | 1374 |
| *Hibiscus cannabinus* L. (Kenaf) | | | | | | | | | | | | | | | | |
| 1 | Seed | 1R,2R | 1.7 | 13.5 | 52.8 | 1.0 | 1.2 | 4.0 | 0.1 | 1.7 | 6.5 | 0.1 | 7.2 | 0.1 | | 1377 |
| *Lilium longiflorum* Thunb. (Trumpet Lily) | | | | | | | | | | | | | | | | |
| 1 | Pollen | HPLC | 0.9 | | 20.3 | 42.7 | | | | | | | 4.3 | 10.3[a] | 6.9 | 1769 |
| *Nicotiana tabacum* L. (Tobacco) | | | | | | | | | | | | | | | | |
| 1 | Cell culture | AgTLC | | 3.9 | 79.2 | 16.9 | | | Trace | | Trace | Trace | Trace | Trace | | 1495 |
| *Oryza sativa* L. (Rice) | | | | | | | | | | | | | | | | |
| 1 | Bran, glutinous | AgTLC | | 22.3 | 39.5 | | (18:2/18:1, 6.0) | | | 9.9 | 13.9 | | 8.4 | | | 1845 |
| 1 | Bran, glutinous | 1R,2R | | 20.1 | 36.9 | | (18:2/18:1, 3.4) | | | 6.4 | 11.7 | | 6.3 | | | 1845 |
| 1 | Bran, nonglutinous | 1R,2R | | 29.4 | 37.9 | | (18:2/18:1, 4.5) | | | 8.1 | 14.4 | | 5.7 | | | 1845 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Bran, nonglutinous | 1R,2R | | 22.6 | 33.6 | | (18:2/18:1, 2.6) | | | 8.8 | 13.1 | | 3.7 | | | 1845 |
| *Phaseolus coccineus* L. (Scarlet Runner Bean) | | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | 0.9 | 8.8[b] | 40.6 | 34.3 | 0.5 | | 3.9 | 0.3 | 2.1 | 1.8 | 2.6 | 3.2 | 1.1 | 1693 |
| *Phaseolus vulgaris* L. (Kidney Bean) | | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | 0.7 | 8.6[b] | 26.2 | 40.1 | 0.8 | | 4.1 | 2.0 | 3.5 | 3.7 | 3.9 | 4.0 | 2.4 | 1693 |
| *Pisum sativum* L. (Pea) | | | | | | | | | | | | | | | | |
| 1 | Seed | AgTLC | 6.5 | 24.4 | 43.5 | 3.2 | 3.7 | 8.7[c] | | | 6.8 | | 3.2 | | | 1904 |
| 1 | Seed | 1R,2R | 5.5 | 21.4 | 42.2 | 2.4 | 2.5 | 4.9 | 0.3 | 2.7 | 5.3 | 0.3 | 2.8 | 0.2 | | 1904 |
| 1 | Seed | HPLC | 0.7 | 21.6[b] | 47.5 | 2.6 | 2.8 | | 0.3 | 1.8 | 7.1 | 5.4 | 6.5 | 2.1 | 1.7 | 1693 |
| 1 | Leaf | HPLC | | | 44.9 | 39.9 | | | 6.4 | | 0.9 | | 3.3 | 4.6 | | 1983 |
| *Rauvolfia serpentina* Benth. ex Kurz (Indian Snakeroot) | | | | | | | | | | | | | | | | |
| 1 | Cell culture | AgTLC | | | 92.3 | 1.6 | 0.1 | 5.4 | Trace | 0.6 | | | Trace | | | 1495 |
| *Secale cereale* L. (Rye) | | | | | | | | | | | | | | | | |
| 2 | Grain (1) | HPLC | | 8 | 44 | 7 | | | | 1 | 9 | 3 | 18 | 7 | 1 | 1957 |
| | Grain (2) | HPLC | | 10 | 41 | 3 | | | | 4 | 16 | | 22 | 4 | 1 | 1957 |
| *Solanum tuberosum* L. (Potato) | | | | | | | | | | | | | | | | |
| 1 | Tuber, microsomes | HPLC | | | 73.7 | 22.2 | | Trace | Trace | | | | 4.1 | | | 1983 |
| *Vicia faba* L. (Broad Bean) | | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | 0.6 | 16.7[b] | 60.6 | 2.0 | 1.2 | | 0.4 | 2.0 | 8.8 | 0.3 | 6.8 | 0.1 | <0.1 | 1693 |
| *Vigna angularis* (Willd.) Ohwi and Ohashi (Adzuki Bean) | | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | | 8.5[b] | 60.9 | 18.5 | | | 2.0 | | 3.1 | 0.7 | 3.6 | 2.3 | 0.5 | 2051 |
| 1 | LEAf | HPLC | | 4.1[b] | 30.1 | 54.4 | | | 3.1 | | 0.3 | 4.2[d] | | 0.1 | 0.6 | 2051 |
| 1 | Root | HPLC | | 7.3[b] | 45.9 | 29.7 | | | 2.1 | | 0.7 | 5.0[d] | | 7.5 | 1.9 | 2051 |
| | Similar data reported for PI molecular species in cotyledon, leaf, hypocotyl, and root tissue of adzuki bean cell culture | | | | | | | | | | | | | | | 2052 |
| *Zea mays* L. (Corn) | | | | | | | | | | | | | | | | |
| 1 | Seedling coleoptile microsome | HPLC | | 4.2 | 75.4 | 4.6 | | 3.4 | | | 7.4 | | 5.0 | | | 2079 |
| 1 | –, plasma membrane | HPLC | | 6.6 | 82.0 | 3.6 | | | | | | | 7.8 | | | 2079 |
| *Zea mays* L. ssp. *saccharata* Sturt (Sweet Corn) | | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | | 10 | 41 | 13 | | | | 3 | 11 | | 19 | 3 | | 2086 |

[a]Including 18:3/18:2 (LnL).
[b]Including 18:0/18:2 (SL).
[c]Including 18:1/18:1 (OO).
[d]Including 18:2/18:2 (LL).

PLPI [R.N. 126253-19-8]: Spectra: FAB-MS,[2135] FAB-MS/MS (fig.),[2136] MALDI FT-ICR-MS (fig.).[1370] Chromatography: HPLC,[2101] HPLC-MS (fig.)[2106], HPLC-MS/MS.[1415]

1-Palmitoyl-2-linolenoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (PLnPI), 16:0/18:3 PI, $C_{43}H_{77}O_{13}P$. D-myo-*Inositol, [R-(Z,Z,Z)]-1-[3-[(1-oxohexadecyl)oxy]-2-[(1-oxo-9,12,15-octadecatrienyl)-oxy]propyl Hydrogen Phosphate]*.

PLnPI [R.N. 124264-81-9]: Spectra: FAB-MS,[2135] FAB-MS/MS.[2136] Chromatography: HPLC,[2101] HPLC-MS,[2106] HPLC-MS/MS.[1415]

1-Stearoyl-2-oleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (SOPI), 18:0/18:1 PI, $C_{45}H_{85}O_{13}P$. D-myo-*Inositol, [R-(Z)]-1-[2-[(1-oxo-9-octadecenyl)oxy]-3-[(1-oxooctadecyl)oxy]propyl Hydrogen Phosphate]*.

SOPI [R.N. 58116-17-9]: FAB-MS,[2135] HPLC.[2100]

$NH_4C_{45}H_{84}O_{13}P$ [R.N. 58165-70-1]: mp 174-176 °C, $[\alpha]_D^{20}$ +6.4° ($CHCl_3$), +7.3° ($CHCl_3$/methanol 2:2). Spectra: IR.[2347] Chromatography: TLC.[2347]

1-Stearoyl-2-linoleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (SLPI), 18:0/18:2 PI, $C_{45}H_{83}O_{13}P$. D-myo-*Inositol, [R-(Z,Z)]-1-[2-[(1-oxo-9,12-octadecadienyl)oxy]-3-[(1-oxooctadecyl)oxy]propyl Hydrogen Phosphate]*.

SLPI [R.N. 83674-12-8]: Spectra: FAB-MS,[2135] FAB-MS/MS.[2136] Chromatography: HPLC,[2348] HPLC-MS,[2106] HPLC-MS/MS.[1415]

1-Stearoyl-2-linolenoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (SLnPI), 18:0/18:3 PI, $C_{45}H_{81}O_{13}P$. D-myo-*Inositol, [R-(Z,Z,Z)]-1-[2-[(1-oxo-9,12,15-octadecatrienyl)oxy]-3-[(1-oxooctadecyl)oxy]-propyl Hydrogen Phosphate]*.

SLnPI [R.N. 182509-37-1]: Spectra: FAB-MS,[2135] FAB-MS/MS.[2136] Chromatography: HPLC.[1983]

1,2-Dioleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (DOPI), 18:1/18:1 PI, $C_{45}H_{83}O_{13}P$. D-myo-*Inositol, [R-(Z,Z)]-1-[2,3-bis-[(1-oxo-9-octadecenyl)oxy]propyl Hydrogen Phosphate]*.

DOPI [R.N. 103065-23-2]: Spectra: IR, $^1$H NMR, FAB-MS (fig.),[2342] FAB-MS/MS.[2136]

1-Oleoyl-2-linoleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (OLPI), 18:1/18:2 PI, $C_{45}H_{81}O_{13}P$. D-myo-*Inositol, [R-(Z,Z,Z)]-1-[2-[(1-oxo-9,12-octadecadienyl)oxy]-3-[(1-oxo-9-octadecenyl)-oxy]propyl Hydrogen Phosphate]*.

OLPI [R.N. 182509-35-9]: Spectra: FAB-MS/MS.[2136] Chromatography: HPLC,[2101] HPLC-MS.[2106]

1-Oleoyl-2-linolenoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (OLnPI), 18:1/18:3 PI, $C_{45}H_{79}O_{13}P$. D-myo-*Inositol, [R-(all Z)]-1-[2-[(1-oxo-9,12,15-octadecatrienyl)oxy]-3-[(1-oxo-9-octadecenyl)-oxy]propyl Hydrogen Phosphate]*.

OLnPI [R.N. 124211-31-0]: HPLC.[2051]

1,2-Dilinoleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (DLPI), 18:2/18:2 PI, $C_{45}H_{79}O_{13}P$. D-myo-*Inositol, [R-(all Z)]-1-[2,3-bis-[(1-oxo-9,12-octadecadienyl)oxy]propyl Hydrogen Phosphate]*.

DLPI [R.N. 122921-66-8]: Spectra: FAB-MS/MS.[2136] Chromatography: HPLC,[2348] HPLC-MS.[2106]

1-Linoleoyl-2-linolenoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (LLnPI), 18:2/18:3 PI, $C_{45}H_{77}O_{13}P$. D-myo-*Inositol, [R-(all Z)]-1-[2-[(1-oxo-9,12-octadecadienyl)oxy]-3-[(1-oxo-9,12,15-octadecatrienyl)oxy]propyl Hydrogen Phosphate]*.

LLnPI [R.N. 126936-49-0]: HPLC.[1983]

1,2-Dilinolenoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (DLnPI), 18:3/18:3 PI, $C_{45}H_{85}O_{13}P$. D-myo-*Inositol, [R-(all Z)]-1-[2,3-bis-[(1-oxo-9,12,15-octadecatrienyl)oxy]propyl Hydrogen Phosphate]*.

DLnPI [R.N. 124211-30-9]: HPLC.[1769]

### Molecular Species Composition

The molecular species composition of phosphatidylinositol in plants, determined by any of the methods described on pages 168–171, is given in Table 4-12.

### Synthesis

DPPI may be prepared (a) by the reaction of 2,3,4,5,6-penta-*O*-benzyl-D-*myo*-inositol with phenyl phosphorodichloridate and 1,2-dipalmitoyl-*sn*-glycerol[2345] or with the phosphoramidite of 1,2-dipalmitoyl-*sn*-glycerol in the presence of tetrazole,[2341] (b) by phosphorylation of 2,3,4,5-di-*O*-cyclohexylidene-6-*O*-(2-trimethylsilylethoxy)methyl-D-*myo*-inositol with methyl *N,N*-diisopropylaminophosphorochloridite followed by reaction with 1,2-dipalmitoyl-*sn*-glycerol in the presence of tetrazole,[2349] (c) by condensation of 1,2-dipalmitoyl-*sn*-glycero-3-(sodium phenyl phosphate) with 2,3,5,6-di-*O*-cyclohexylidene-D-*myo*-inositol [2343] or its 4-(5,6-dihydro-4-methoxy-2*H*-pyran) derivative[2344] in the presence of the triazole MSNT, or (d) by acylation of tetrahydropyran-protected *sn*-glycero-3-phospho-D-*myo*-inositol with palmitic anhydride.[2342] POPI may be prepared by the reaction of silver 2,3,4,5,6-penta-*O*-acetyl-D-*myo*-inositol-1-benzyl phosphate with 1-palmitoyl-2-oleoyl-*sn*-glycero-3-iodohydrin.[2346] PLPI may be prepared by acylation of tetrahydropyran-protected PHPI with linoleoyl chloride.[2350] SOPI may be prepared by the reaction of 2,3,4,5,6-penta-*O*-acetyl-D-*myo*-inositol-1-dihydrogen phosphate with 2-oleoyl-1-stearoyl-*sn*-glycerol in the presence of mesitylenesulfonyl chloride.[2347] Finally, DOPI may be prepared by acylation of tetrahydropyran-protected *sn*-glycero-3-phospho-D-*myo*-inositol with oleic anhydride in the presence of 4-dimethylaminopyridine.[2342]

## Lysophosphatidylinositols

### Physical Properties

1-Palmitoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (PHPI), 16:0 LPI, $C_{25}H_{49}O_{12}P$. D-myo-*Inositol, (R)-1-[2-Hydroxy-3-[(1-oxohexadecyl)oxy]propyl Hydrogen Phosphate]*.

PHPI [R.N. 112573-74-7; see also 106182-20-1]: Spectra: $^1$H NMR,[2351] FAB-MS/MS (fig.).[2352] Chromatography: TLC,[2353] silica gel column.[2351]

$NH_4C_{25}H_{48}O_{12}P$: Solid, IR.[2351]

1-Linoleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (LHPI), 18:2 LPI, $C_{27}H_{49}O_{12}P$. *D*-myo-*Inositol, [R (Z,Z)]-1-[2-Hydroxy-3-[(1-oxo-9,12-octadecadienyl)oxy]propyl Hydrogen Phosphate]*.

LHPI [R.N. 124330-66-1]: Spectra: FAB-MS/MS.[2352] L-Isomer [R.N. 142508-96-1]: White solid. Spectra: $^{1}H$ and $^{13}C$ NMR, FAB-MS/MS. Chromatography: TLC, HPLC.[2354]

### Synthesis

PHPI may be prepared by phosphorylation of 2,3,4,5,6-penta-*O*-acetyl-D-*myo*-inositol with methyl *N*,*N*-diisopropylaminophosphorodichloridite followed by reaction with 1-palmitoyl-2-benzyl-*sn*-glycerol in the presence of tetrazole.[2351]

LHPI and HLPI: Syntheses of the L-isomers are available.[2354]

## Phosphatidylinositol Phosphates

### Occurrence

The occurrence of polyphosphoinositides in plant cells was first demonstrated in 1985 by Boss and Massel,[1359] who isolated PI, PIP, and $PIP_2$ from wild carrot cell cultures in 93:1.7:0.8% yield, based on recovered inositol. This ratio proved to be representative of a variety of plant species (Table 4-13). In contrast to animal cells, the amount of $PIP_2$ is almost always smaller than that of PIP, and their sum total is usually very low relative to PI. Also, because the amounts of PIP and $PIP_2$ are so small, the only quantitative method available to date is radiolabeling, which assumes that isotopic equilibrium has been reached prior to analysis. The preferred precursor is D-*myo*-[2-$^{3}H$]-inositol because it labels PIs exclusively, but [2-$^{3}H$]-glycerol, [$^{32}P$]$P_i$ and [$\gamma$-$^{32}P$]-ATP, [$^{14}C$]-*myo*-inositol, and [1-$^{14}C$]-acetate have also been employed.

**Table 4-13** Phosphatidylinositol Phosphates in Plants*

| No. | Plant part | Method | LPI | LPIP | PI | PIP | $PIP_2$ | References |
|---|---|---|---|---|---|---|---|---|
| *Brassica napus* L. ssp. *oleifera* L. (Winter Rape) | | | | | | | | |
| 1 | Leaf | 2-[$^{3}H$]-Ins | | | 32 | 9 | 3 | 1326 |
| *Brassica oleracea* L. ssp. *botrytis* L. (Cauliflower) | | | | | | | | |
| 1 | Cotyledon | [$^{32}P$]$P_i$ | | | 76.7 | 16.7 | 6.6 | 1244 |
| *Catharanthus roseus* (L.) G. Don (Madagascar Periwinkle) | | | | | | | | |
| 1 | Cell culture | 2-[$^{3}H$]-Ins | | | 92 | 5 | 2.5 | 2355 |
| 1 | Cell culture[a] | [$^{32}P$]$P_i$ | | | 92 | 7 | 1 | 2356 |
| *Daucus carota* L. (Wild Carrot) | | | | | | | | |
| 1 | Cell culture[b] | 2-[$^{3}H$]-Ins | 7.4 | 4.7 | 76.0 | 7.0 | 0.58 | 2357 |
| 1 | –, plasma membrane[b] | 2-[$^{3}H$]-Ins | 4.5 | 18.9 | 54.0 | 14.2 | 1.3 | 2357 |
| 1 | –, microsomes and mitochondria[b] | 2-[$^{3}H$]-Ins | 18.6 | 2.0 | 73.5 | 2.7 | 0.3 | 2357 |
| 1 | –, protoplasts[b] | 2-[$^{3}H$]-Ins | 11.10 | 1.33 | 80.43 | 4.87 | 0.67 | 2353 |
| *Dianthus caryophyllus* L. (Carnation) | | | | | | | | |
| 1 | Flower petal | 2-[$^{3}H$]-Ins, [$^{32}P$]$P_i$ | | | 91.5 | 8.3 | 0.23 | 1202 |

**Table 4-13** Phosphatidylinositol Phosphates in Plants*—cont'd

| No. | Plant part | Method | LPI | LPIP | PI | PIP | $PIP_2$ | References |
|---|---|---|---|---|---|---|---|---|
| *Glycine max* (L.) Merr. (Soybean) | | | | | | | | |
| 1 | Bean, hypocotyl | 2-[$^3$H]-Ins | | | 55 | 2 | 2 | 2358 |
| 1 | –, microsomal membrane | 2-[$^3$H]-Ins | | | 95 | 0 | 0 | 2358 |
| 1 | Cell culture | 2-[$^3$H]-Ins | | | 91 | 9 | Trace | 1221 |
| *Helianthus annuus* L. (Sunflower) | | | | | | | | |
| 1 | Hypocotyl plasma membrane[a] | [$^{32}$P]$P_i$ | | | 78.8 | 8.1 | 4.0 | 2359 |
| *Hordeum vulgare* L. (Barley) | | | | | | | | |
| 1 | Seed, aleurone layer | 2-[$^3$H]-Ins | | | 99.1 | 0.7 | 0.2 | 1204 |
| 1 | Seed, aleurone layer | [$^{32}$P]$P_i$ | | | 100 | 10 | 1 | 1204 |
| *Lilium longiflorum* Thunb. (Trumpet Lily) | | | | | | | | |
| 1 | Pollen[a] | 2-[$^3$H]-Ins, | | | 96 | 3 | 1 | 2360 |
| 1 | Pollen[a] | [$^{32}$P]$P_i$ | | | 98.5 | 1 | 0.5 | 2360 |
| *Lycopersicon esculentum* Mill. (Tomato) | | | | | | | | |
| 1 | Leaf[c] | [$^{32}$P]$P_i$ | | | 12.7 | 12.6 | 1.6 | 2361 |
| 1 | Root | TLC | | | ++ | ++ | + | 1231 |
| 1 | Cell culture | 2-[$^3$H]-Glycerol | | | 9 | 1.1 | 0.04 | 2362 |
| *Nicotiana tabacum* L. (Tobacco) | | | | | | | | |
| 1 | Cell culture | 2-[$^3$H]-Ins | | | 96 | 3 | 1 | 1200 |
| *Petroselinum crispum* Nym. (Parsley) | | | | | | | | |
| 1 | Cell culture [d] | 2-[$^3$H]-Ins | | | 84 | 6 | 8 | 1221 |
| *Petunia hybrida* hort. (Petunia) | | | | | | | | |
| 1 | Pollen[a] | 2-[$^3$H]-Ins or [$^{32}$P]$P_i$ | | | 100 | 0 | 0 | 2363 |
| *Peucedanum verticillare* (L.) Koch | | | | | | | | |
| 1 | Callus culture | TLC | | | 35.46 | 4.88 | 4.32 | 2364 |
| *Pisum sativum* L. (Peas) | | | | | | | | |
| 1 | Leaf | 2-[$^3$H]-Ins | | | | + | 0.04 | 1201 |
| *Saccharum* spp. (Sugarcane) | | | | | | | | |
| 1 | Leaf[c] | [$^{32}$P]$P_i$ | | | 23.1 | 6.3 | 2.5 | 2361 |
| *Samanea saman* (Jacq.) Merr. (Raintree) | | | | | | | | |
| 1 | Leaf, pulvini | HPLC | | | | 0.3 | <0.02 | 1418 |
| *Solanum melongena* L. (Brinjal, Eggplant) | | | | | | | | |
| 1 | Leaf[c] | [$^{32}$P]$P_i$ | | | 20.3 | 15.9 | 1.6 | 2361 |
| *Spirodela polyrrhiza* L. (Giant Duckweed) | | | | | | | | |
| 1 | Whole plant | 2-[$^3$H]-Ins | | | 15.2 | 59.2[e] | 4.2[f] | 1362 |
| *Zea mays* L. (Corn, Maize) | | | | | | | | |
| 1 | Leaf[c] | [$^{32}$P]$P_i$ | | | 13.8 | 8.9 | 3.6 | 2361 |
| 1 | Coleoptile | [$^{14}$C]-Ins | | | 92.3 | 7.0 | 0.7 | 2365 |
| 1 | Coleoptile | 1-[$^{14}$C]-Acetate | | | 93.4 | 4.6 | 2.0 | 2365 |

*Molar ratio of PI subclasses.
[a]Percentage of total PI.
[b]Percentage of recovered 2-[$^3$H]-Ins.
[c]Percentage of total PL.
[d]nmol/g fwb.
[e]57.6 PI(4)P and 1.6 PI(3)P.
[f]3.6 PI(4,5)$P_2$ and 0.6 PI(3,4)$P_2$.

## Separation and Analysis

Extraction of the phosphoinositides from the radiolabeled plant tissue is usually performed by a modified Folch procedure, using, for example, 1:2 chloroform/methanol containing 1% conc. HCl.[2356] The inclusion of acid is critical because at neutral pH, PIP and $PIP_2$ are not extracted into the organic phase.[1196a] The phosphoinositides are separated by TLC in the order PI > PIP > $PIP_2$ and quantitated by radiography as follows:

> *Wild carrot cells . . . (0.3 g fresh wt) were labeled overnight (19 h) with* myo-*[2-$^3$H]inositol (19.0 Ci/mmol) 16.7 μCi/g fresh wt. The cells were harvested on filter paper and washed with 100 mL water to remove the medium. The polyphosphoinositides were extracted . . . with . . . 1.5 mL $CHCl_3$:MeOH (1:2), 0.5 mL of 2.4*N *HCl, 0.5 mL of $CHCl_3$, and 0.5 mL of 0.1*N *EDTA. The mixture was centrifuged and the lower phase collected. The upper phase was reextracted twice with $CHCl_3$ and the extracts combined and backwashed twice with MeOH:1*N *HCl (1:1). The $CHCl_3$ layer was collected and dried (in vacuo) . . . . The dried extracts were reconstituted in $CHCl_3$/MeOH (3:1) and spotted on . . . high performance, silica gel LKS plates . . . which had been impregnated with 1 % potassium oxalate, dipping the preabsorbent area in the oxalate first, and dried (110 C) for 1 h. The plates were run for 2.5 h in $CHCl_3$:MeOH:4* N *$NH_4OH$, 90:70:20 and scraped and counted . . . in a Beckmann LS 7000 scintillation counter.*
>
> Boss, W. F.; Massel, M. O., "Polyphosphoinositides are Present in Plant Tissue Culture Cells", *Biochem. Biophys. Res. Commun.* **1985**, *132*(3), 1018–1023,[1359] reprinted by permission of Elsevier, © 1985.

Separation of the phosphoinositides has also been carried out by HPLC on an amino-NP silica column with a 0 → 0.8 *M* ammonium acetate gradient. The compounds, monitored by liquid scintillation, were eluted in the order PI > PIP > $PIP_2$.[1418]

A protocol for separating all known isomers of PIP and $PIP_2$ by thin-layer chromatography on boric acid-impregnated HPTLC plates has been described.[2366]

## Phosphoinositide Isomers

That the PIP and $PIP_2$ of plant species are in fact PI(4)P and PI(4,5)$P_2$ as in animal systems has been verified by chemical degradation methods. Removal of the acyl and glyceryl substituents from PIP leaves an inositol bisphosphate identified as Ins(1,4)$P_2$, and similar treatment of $PIP_2$ leaves an inositol trisphosphate identified as Ins(1,4,5)$P_3$.[1201] Brearley and Hanke[1207,1362] later detected PI(3)P and PI(3,4)$P_2$ (but not PI(3,4,5)$P_3$) in *Spirodela polyrrhiza* in addition to the PI(4)P and PI(4,5)$P_2$.

## Molecular Species

PIP appears to have the same molecular species distribution as PI. HPLC analysis of the PIP in maize coleoptile shows the principal species to be 16:0:18:2 (59.0%) together with smaller amounts of 16:0/18:1, 16:0/18:3, 18:0/18:2, 18:2/18:2, and traces of 18:1/18:2 species.[2365]

## Physical Properties

1,2-Dipalmitoyl-*sn*-glycero-3-phospho-D-*myo*-inositol 3-phosphate (DPPI(3)P), 16:0/16:0 PIP, $C_{41}H_{80}O_{16}P_2$. D-myo-*Inositol, (R)-1-[2,3-bis[(1-oxohexadecyl)oxy]propyl Hydrogen Phosphate] 3-Dihydrogen Phosphate.*

DPPI(3)P [R.N. 165689-81-6]: White solid, mp 108-110 °C, $[\alpha]_D^{22}$ +0.7° ($CHCl_3$/methanol). [2368] Spectra: $^1H$ and $^{31}P$ NMR,[2369] FAB-MS.[2370]

$NH_4C_{41}H_{79}O_{16}P_2$: LC-MS.[2369]

1,2-Dipalmitoyl-*sn*-glycero-3-phospho-D-*myo*-inositol 4-phosphate (DPPI(4)P), 16:0/16:0 PIP, $C_{41}H_{80}O_{16}P_2$. D-myo-*Inositol, (R)-1-[2,3-bis[(1-oxohexadecyl)oxy]propyl Hydrogen Phosphate] 4-Dihydrogen Phosphate.*

DPPI(4)P [R.N. 57606-15-2]: White solid. Spectra: $^1H$ and $^{31}P$ NMR.[2343]

$(NH_4)_3C_{41}H_{77}O_{16}P_2$ [R.N. 161105-05-1]: mp 151-154 °C, $[\alpha]_D^{20}$ +4.5° ($CHCl_3$/methanol), soluble in $CHCl_3$, insoluble in acetone; ORD (fig.). Spectra: IR (fig.). Chromatography: TLC.[2371]

1,2-Dipalmitoyl-*sn*-glycero-3-phospho-D-*myo*-inositol 3,4-bisphosphate (DPPI(3,4)P), 16:0/16:0 $PIP_2$, $C_{41}H_{81}O_{19}P_3$. D-myo-*Inositol, (R)-1-[2,3-bis[(1-oxohexadecyl)oxy]propyl Hydrogen Phosphate] 3,4-bis(Dihydrogen Phosphate).*

DPPI(3,4)$P_3$ [R.N. 165883-85-2]: White solid, mp 62-65 °C, $[\alpha]_D^{23}$ +1.9° ($CHCl_3$).[2370] Spectra: $^1H$ and $^{31}P$ NMR,[2370] FAB-MS,[2370] MALDI TOF-MS.[2372]

$Na_5C_{41}H_{76}O_{19}P_3$ [R.N. 195318-65-1]: $[\alpha]_D^{22}$ +6.8° ($H_2O$).[2368]

$(NH_4)_5C_{41}H_{76}O_{19}P_3$ [R.N. 165883-85-2]: Spectra: $^1H$ and $^{31}P$ NMR. Chromatography: LC-MS.[2369]

1,2-Dipalmitoyl-*sn*-glycero-3-phospho-D-*myo*-inositol 4,5-bisphosphate (DPPI(4,5)$P_2$), 16:0/16:0 $PIP_2$, $C_{41}H_{81}O_{19}P_3$. D-myo-*Inositol, (R)-1-[2,3-bis[(1-oxohexadecyl)oxy]propyl Hydrogen Phosphate] 4,5-bis(Dihydrogen Phosphate).*

DPPI(4,5)$P_2$ [R.N. 120595-88-2]: No data.

$Na_5C_{41}H_{76}O_{19}P_3$ [R.N. 183623-41-8]: White solid. Spectra: $^1H$ and $^{31}P$ NMR, MALDI MS.[2373]

$(C_6H_{11}NH_3)_5C_{41}H_{76}O_{19}P_3$ [R.N. 120664-89-3]: Spectra: $^1H$, $^{13}C$, and $^{31}P$ NMR.[2374]

## Synthesis

DPPI(3)P may be prepared (a) by phosphorylation of a 2,4,5,6-protected DPPI with dibenzyl *N,N*-diisopropylphosphoramidite with 1*H*-tetrazole,[2375] or (b) by stepwise reaction of a 2,4,5,6-protected 1D-*myo*-inositol-3-dibenzyl phosphate with methyl *N,N*-diisopropylphosphoramidochloridite followed by 1,2-dipalmitoyl-*sn*-glycerol [2369] or vice versa.[2370] DPPI(4)P may be prepared (a) by phosphorylation of a 2,3,5,6-protected DPPI with diphenyl *N,N*-diethylphosphoramidite in the presence of 1*H*-tetrazole,[2343] (b) by condensation of a 2,3,5,6-protected 1D-*myo*-inositol-4-diphenyl phosphate with DPPA in the presence of mesitylenesulfonyl chloride,[2371] (b) by the reaction of a 2,3,5,6-protected 1D-*myo*-inositol-3-dibenzyl phosphate with benzyl 1,2-dipalmitoyl-*sn*-glycero-*N,N*-diisopropylphosphoramidite in the presence of 1*H*-tetrazole.[2375] DPPI(3,4)$P_2$ may be prepared by condensation of a 2,5,6-protected 1D-*myo*-inositol-3,4-bis(dibenzyl phosphate) (a) with benzyl 1,2-dipalmitoyl-*sn*-glycero-*N,N*-diisopropylphosphoramidite in the presence of 1*H*-tetrazole,[2368,2370] (b) with methyl *N,N*-diisopropylphosphoramidochloridite in the presence

of 1*H*-tetrazole,[2369] or (c) with dibenzyl 1,2-dipalmitoyl-*sn*-glycerophosphite and pyridinium perbromide.[2376] DPPI(4,5)$P_2$ may be prepared by phosphorylation of a 2,3,6-protected DPPI with dibenzyl *N,N*-diisopropylphosphoramidite in the presence of 1*H*-tetrazole.[2373,2374]

### Phosphorylation

Enzymic phosphorylation of PIP with PIP kinase yields $PIP_2$, as shown in Fig. 4-1, but nonenzymic phosphorylation with ATP in the presence of a bivalent metal ion such as Ca(II) or Mn(II) results in a different $PIP_2$, the 4-pyrophosphate.[2367]

## Lysophosphatidylinositol Phosphates

### Physical Properties

1-Palmitoyl-*sn*-glycero-3-phospho-D-*myo*-Inositol 4-Phosphate (16:0 LPI(4)P), $C_{25}H_{50}O_{15}P_2$. *D*-myo-*Inositol, (R)-1-[2-Hydroxy-3-[(1-oxohexadecyl)oxy]propyl Hydrogen Phosphate] 4-Dihydrogen Phosphate.*

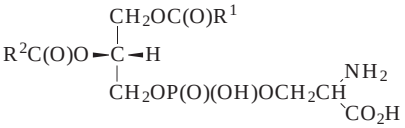
PHPI(4)P [R.N. 129485-82-1]: Spectra: FAB-MS/MS.[2352] Chromatography: TLC.[2353]

1-Linoleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol 4-phosphate (18:2 LPI(4)P), $C_{27}H_{50}O_{15}P_2$. *D*-myo-*Inositol, [R-(Z,Z)]-1-[2-Hydroxy-3-[(1-oxo-9,12-octadecadienyl)oxy] propyl Hydrogen Phosphate] 4-Dihydrogen Phosphate.*

LHPI(4)P: Spectra: FAB-MS/MS.[2352] Chromatography: TLC.[2353]

# PHOSPHATIDYLSERINES

This group comprises the phosphatidylserines (PS) and lysophosphatidylserines (LPS).




PS, $R^1 = R^2 =$ alkyl
2-LPS, $R^1 =$ alkyl, $R^2 = H$

## Phosphatidylserines

### Physical Properties

1,2-Dipalmitoyl-*sn*-glycero-3-phospho-L-serine (DPPS), 16:0/16:0 PS, $C_{38}H_{74}NO_{10}P$. *L-Serine, (R)-2,3-bis[(1-Oxohexadecyl)oxy]propyl Hydrogen Phosphate (Ester).*

DPPS [R.N. 40290-42-4; see also 3036-82-6]: Fine white powder, mp 149-150 °C[2377] or 153-155 °C[2378]; $[\alpha]_D^{20}$ +5.3° ($CHCl_3$),[2377] +12.5° ($CHCl_3$) [2211] or +17.7° (benzene),[2378] $[\alpha]_D^{22}$ +5.5° ($CHCl_3$/MeOH/$H_2O$)[2379]; soluble in chloroform and insoluble in acetone[2377]; p$K_a$ 2.7 (potentiometric)[2380] and 4.6 (FTIR)[2381]; $T_C$ and DSC (fig.).[2256] Spectra: IR,[2377] FTIR,[2382] $^1$H NMR,[2274] $^{13}$C and $^{31}$P NMR,[2211] FAB-MS,[2274] FD-MS (fig.),[2140] CI-MS,[2264] MALDI-MS (fig.),[2178] FAB-MS/MS (fig.),[2383] MALDI FT-ICR-MS/MS (fig.).[1370] Chromatography: TLC,[2211] preparative TLC,[2379] HPLC,[2239] silicic acid column,[2211] DEAE cellulose column.[2379] $NaC_{38}H_{73}NO_{10}P$: LSI-MS.[2239]

1-Palmitoyl-2-oleoyl-*sn*-glycero-3-phospho-L-serine (POPS), 16:0/18:1 PS, $C_{40}H_{76}NO_{10}P$. *L-Serine, [R-(Z)]-3-[(1-Oxohexadecyl)oxy]-2-[(1-oxo-9-octadecenyl)oxy]propyl Hydrogen Phosphate (Ester).*

POPS [R.N. 40290-44-6; see also 79980-16-8]: mp 127-130 °C, $[\alpha]_D^{20}$ +6.2° ($CHCl_3$).[2377] Spectra: IR (fig.),[2384] Raman,[2385] ESR,[2184] LSIMS (Na salt).[2239] Chromatography: TLC,[2377] HPLC,[2110] LC-MS (fig.),[2106] silicic acid column.[2377] Electrophoresis: CE (fig.).[2181]

$NaC_{40}H_{75}NO_{10}P$: LSI-MS.[2239]

$NH_4C_{40}H_{75}NO_{10}P$: $^{31}P$ NMR (fig.).[2384]

1-Palmitoyl-2-linoleoyl-*sn*-glycero-3-phospho-L-serine (PLPS), 16:0/18:2 PS, $C_{40}H_{74}NO_{10}P$. *L-Serine, [R-(Z,Z)]-3-[(1-Oxohexadecyl)oxy]-2-[(1-oxo-9,12-octadecadienyl)oxy]propyl Hydrogen Phosphate (Ester).*

PLPS [R.N. 91178-24-4; see also 120574-71-2]: FAB-MS, CI-MS.[2264]

1-Stearoyl-2-oleoyl-*sn*-glycero-3-phospho-L-serine (SOPS), 18:0/18:1 PS, $C_{42}H_{80}NO_{10}P$. *L-Serine, [R-(Z)]-2-[(1-Oxo-9-octadecenyl)oxy]-3-[(1-oxooctadecyl)oxy]propyl Hydrogen Phosphate (Ester).*

SOPS [R.N. 124262-03-7; see also 76091-35-5]: Spectra: FAB-MS,[2135] FAB-MS/MS (fig.),[2386] CID-MS/MS (fig.).[2265] Chromatography: HPLC,[1809] LC-MS.[2106]

1-Stearoyl-2-linoleoyl-*sn*-glycero-3-phospho-L-serine (SLPS), 18:0/18:2 PS, $C_{42}H_{78}NO_{10}P$. *L-Serine, [R-(Z,Z)]-2-[(1-Oxo-9,12-octadecadienyl)oxy]-3-[(1-oxooctadecyl)oxy]propyl Hydrogen Phosphate (Ester).*

SLPS [R.N. 132014-81-4; see also 125874-21-7]: Spectra: FAB-MS.[2135]

1,2-Dioleoyl-*sn*-glycero-3-phospho-L-serine (DOPS), 18:1/18:1 PS, $C_{42}H_{78}NO_{10}P$. *L-Serine, [R-(Z,Z)]-2,3-bis-[(1-Oxo-9-octadecenyl)oxy]propyl Hydrogen Phosphate (Ester).*

DOPS [R.N. 70614-14-1; see also 6811-55-8]: Crystals, mp 165-169 °C, $[\alpha]_D^{22}$ −6.0° ($CHCl_3$), +6.2° ($CHCl_3$/MeOH/$H_2O$), −13.5° (benzene)[2379]; DSC.[2379] Spectra: IR (fig.),[2384] $^1H$ NMR (fig.),[2379] $^{31}P$ NMR (fig.),[2384] LSI-MS.[2239] Chromatography: TLC,[2217] preparative TLC,[2379] HPLC,[2110] LC-MS,[2106] CM-celullose column.[2379]

$BaC_{42}H_{76}NO_{10}P$ [R.N. 71049-19-9]: Softens at 160 °C. Chromatography: TLC, CM-cellulose column.[2379]

1-Oleoyl-2-linoleoyl-*sn*-glycero-3-phospho-L-serine (OLPS), 18:1/18:2 PS, $C_{42}H_{76}NO_{10}P$. *L-Serine, [R-(Z,Z,Z)]-2-[(1-Oxo-9,12-octadecadienyl)oxy]-3-[(1-oxo-9-octadecenyl)oxy]propyl Hydrogen Phosphate (Ester).*

OLPS [R.N. 15045-28-0]: No data available for the *R,L* compound. The *R,DL* isomer (from 1-oleoyl-*sn*-glycero-3-phospho-*N*-phthaloyl-DL-serine and linoleoyl chloride) is an oil, very soluble in benzene, chloroform, ether, and methanol, forming a stable emulsion in water. Spectra: IR (fig.).[2387] Chromatography: TLC, silicic acid column.[2387]

1,2-Dilinoleoyl-*sn*-glycero-3-phospho-L-serine (DLPS), 18:2/18:2 PS, $C_{42}H_{74}NO_{10}P$. *L-Serine, [R-(all Z)]-2,3-bis-[(1-Oxo-9,12-octadecadienyl)oxy]propyl Hydrogen Phosphate (Ester).*

DLPS [R.N. 89616-59-1; see also 14235-22-4]: DSC.[2388] Spectra: $^1H$ and $^{31}P$ NMR.[2388] Chromatography: TLC, CM-cellulose column.[2388] *R,DL-DLPS* (from *sn*-glycero-3-phospho-*N*-phthaloyl-DL-serine and linoleoyl chloride): Waxy solid, IR (fig.), silicic acid

chromatography[2387]; *rac,L-DLPS* (from *O*-phthalimidomethyl-*N*-(*p*-anisyloxycarbonyl)-*rac*-glycerophospho-L-serine and linoleoyl chloride): IR, PC, TLC, DEAE column chromatography[2389]; *rac,DL-DLPS* (from phosphorylated 1,2-dilinoleoyl-*rac*-glycerol and *N*-phthaloyl-*O*-*t*-butyl-DL-serine): IR (fig.), TLC.[2390]

The only PS phospholipids that contain linolenic acid (16:3) reported to date, according to *Chemical Abstracts*, are the phosphatidylserines OLnPS, LLnPS, and DLnPS from algae.[2391]

## Molecular Species Composition

The molecular species composition of phosphatidylserine in plants, determined by any of the methods described on pages 168–171, is given in Table 4-14.

## Synthesis

DPPS may be prepared (a) by phosphorylation of 1,2-dipalmitoyl-*sn*-glycerol with $POCl_3$,[2217] phenyl phosphorodichloridite,[2274] phenyl phosphorodichloridate,[2377] or $PCl_3$/imidazole[2211] followed by reaction with *N*-BOC-L-serine or its *t*-butyl or benzyl ester, (b) by condensation of 1,2-dipalmitoyl-*sn*-glycero-3-iodohydrin with silver phenyl *N*-BOC-*O*-benzyl-L-serine phosphate,[2377] or (c) by acylation of DPPA with *N*-BOC-*O*-benzyl-L-serine in the presence of triisopropylbenzenesulfonyl chloride.[2379] POPS may be prepared by phosphorylation of 1-palmitoyl-2-oleoyl-*sn*-glycerol with phenyl phosphorodichloridate followed by reaction with *N*-BOC-*O*-benzyl-L-serine.[2377] PLPS may be prepared by transesterification of PLPC with L-serine in the presence of phospholipase D.[2264] DOPS may be prepared (a) by phosphorylation of 1,2-dioleoyl-*sn*-glycerol with $POCl_3$ followed by reaction with *N*-BOC-*O*-*t*-butyl-L-serine,[2217] (b) by condensation of DOPA with *N*-BOC-*O*-phthalimidomethyl-L-serine in the presence of triisopropylbenzenesulfonyl chloride,[2379] or (c) by transesterification of DOPC with L-serine in the presence of phospholipase D.[2392] OLPS: None published. The corresponding *R*,DL isomer may be prepared as outlined earlier. DLPS: None published. The corresponding *R*,DL, *rac*,L and *rac*,DL isomers may be prepared as outlined earlier.

## Hydrolysis

The rate and extent of hydrolysis of DPPS by phospholipase B from the mold *P. notatum* is the highest of the phospholipids in the series DPPS > DPPI > DPPA > DPPC > DPPE > DPDPG. The products are *sn*-glycero-3-phospho-L-serine and palmitic acid.[2256] Digestion of DOPS with snake venom phospholipase $A_2$ gives the 2-lyso derivative OHPS, whereas methanolysis with $BF_3$ removes both acyl groups giving >95% oleic acid by GLC analysis.[2379]

**Table 4-14** Molecular Species Composition: Phosphatidylserines (mol%)

| No. | Plant part | Method | 16:0 18:1 | 16:0 18:2 | 18:1 18:2 | 18:1 18:3 | 18:2 18:2 | 18:2 18:3 | Reference |
|---|---|---|---|---|---|---|---|---|---|
| *Daucus carota* L. (Carrot) | | | | | | | | | |
| 1 | Cell suspension culture | AgTLC | 3.4 | 54.7 | 7.4 | | 24.0 | 10.5 | 1648 |

# Lysophosphatidylserines

## Physical Properties

1-Palmitoyl-*sn*-glycero-3-phospho-L-serine (PHPS), 16:0 LPS, $C_{22}H_{44}NO_9P$. L-Serine, *(R)-2-Hydroxy-3-[(1-oxohexadecyl)oxy]propyl Hydrogen Phosphate (Ester)*.
PHPS [R.N. 116947-34-3; see also 75795-82-3]: Spectra: FAB-MS (fig.).[2393]
Chromatography: TLC.[2240]

1-Stearoyl-*sn*-glycero-3-phospho-L-serine (SHPS), 18:0 LPS, $C_{24}H_{48}NO_9P$. *L-Serine, (R)-2-Hydroxy-3-[(1-oxooctadecyl)oxy]propyl Hydrogen Phosphate (Ester)*.
SHPS [R.N. 119786-67-3]: Spectra: FAB-MS,[2135] CID-MS/MS (fig.).[2265]

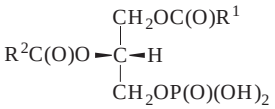
1-Oleoyl-*sn*-glycero-3-phospho-L-serine (OHPS), 18:1 LPS, $C_{24}H_{46}NO_9P$. *L-Serine, [R-(Z)]-2-Hydroxy-3-[(1-oxo-9-octadecenyl)oxy]propyl Hydrogen Phosphate (Ester)*.
OHPS [R.N. 89319-60-8; see also 126575-94-8]: Spectra: FAB-MS (fig.).
Chromatography: TLC.[2394]

## Synthesis

PHPS may be prepared by phosphorylation of 2-benzyl-1-palmitoyl-*sn*-glycerol with $POCl_3$ followed by reaction with *O-t*-butyl-*N*-BOC-L-serine.[2240] OHPS may be prepared by enzymatic hydrolysis of DOPS with snake venom phospholipase $A_2$.[2394]

# PHOSPHATIDIC ACIDS

This group comprises the phosphatidic acids (PA) and two kinds of lysophosphatidic acids (LPA):



PA, $R^1 = R^2 =$ alkyl
1-LPA, $R^1 =$ H, $R^2 =$ alkyl
2-LPA, $R^1 =$ alkyl, $R^2 =$ H

# Phosphatidic Acids

## Physical Properties

1,2-Dipalmitoyl-*sn*-glycero-3-(dihydrogen phosphate) (DPPA), 16:0/16:0 PA, $C_{35}H_{69}O_8P$. *(R)-Hexadecanoic Acid, 1-[(Phosphonooxy)methyl]-1,2-Ethanediyl Ester*.
DPPA [R.N. 7091-44-3]: White powder,[2395] mp 67-68 °C[2396]; $[\alpha]_D^{26}$ +4.0° ($CHCl_3$)[2397]; solubility in g/100 mL at 21 °C: benzene 4.2, ethanol 2.5, methanol 2.0, acetone 1.6, ether 1.5, acetic acid 1.3, petroleum ether <0.001,[2397] DSC.[2398] Spectra: IR,[2399] FTIR,[2400] Raman,[2401] $^1H$ and $^{13}C$ NMR,[118] $^{31}P$ NMR,[2396] CD,[2402] FAB-MS,[2200] FD-MS,[2403] SI-MS,[2239] FAB-MS-MS.[1415] Chromatography: TLC,[2399] HPTLC,[1405] IEC,[2285] SFC,[2156] FPD-GC,[123] GFC,[2404] HPLC-MS/MS.[1415] *rac-DPPA* [R.N.5129-68-0]: mp 62-63 °C, X-ray,[2405] CE.[2324]

$NaC_{35}H_{68}O_8P$: mp 160 °C.[2406]
$Na_2C_{35}H_{67}O_8P$ [R.N. 71065-87-7]: mp 253 °C.[2406]
$CaC_{35}H_{67}O_8P$ [R.N. 71640-91-0]: mp 220 °C, TLC.[2395]
$(NH_4)_2C_{35}H_{67}O_8P$: Solid.[2285]
$C_6H_{11}NH_3C_{35}H_{68}O_8P$: $[\alpha]_D^{20}$ +8.8° ($CHCl_3$).[2404]
$C_5H_5NHC_{35}H_{68}O_8P$ (pyridinium salt): mp 152-153 °C, $[\alpha]_D^{25}$ +3.8° ($CHCl_3$), soluble in benzene and chloroform, insoluble in ethyl acetate, acetone, $CCl_4$, and ether.[2397]

1-Palmitoyl-2-oleoyl-*sn*-glycero-3-(dihydrogen phosphate) (POPA), 16:0/18:1 PA, $C_{37}H_{71}O_8P$. *[R-(Z)]-9-Octadecenoic Acid, 1-[[(1-oxohexadecyl)oxy]methyl]-2-(phosphonooxy)ethyl Ester.*
POPA [R.N. 62600-81-1]: Oil,[2407] DSC.[2408] Spectra: IR,[2407] FAB-MS,[1369] CID-MS/MS (fig.).[2265] Chromatography: TLC,[2407] HPLC,[2103] silica gel column.[2407]

1-Palmitoyl-2-linoleoyl-*sn*-glycero-3-(dihydrogen phosphate) (PLPA), 16:0/18:2 PA, $C_{37}H_{69}O_8P$. *[R-(Z,Z)]-9,12-Octadecadienoic Acid, 1-[[(1-oxohexadecyl)oxy]methyl]-2-(phosphonooxy)ethyl Ester.*
PLPA [R.N. 91190-11-3; see also 120661-81-6]: Spectra: FAB-MS.[1369] Chromatography: HPLC.[2103]
$(NH_4)_2C_{37}H_{67}O_8P$: mp 192-194 °C, $[\alpha]_D$ +4.5° ($CHCl_3$).[2298]

1-Palmitoyl-2-linolenoyl-*sn*-glycero-3-(dihydrogen phosphate) (PLnPA), 16:0/18:3 PA, $C_{37}H_{67}O_8P$. *[R-(Z,Z,Z)]-9,12,15-Octadecatrienoic Acid, 1-[[(1-oxohexadecyl)oxy]methyl]-2-(phosphonooxy)ethyl Ester.*
PLnPA [R.N. 221000-71-1]: Chromatography: HPTLC.[1730]

1-Stearoyl-2-oleoyl-*sn*-glycero-3-(dihydrogen phosphate) (SOPA), 18:0/18:1 PA, $C_{37}H_{75}O_8P$. *[R-(Z)]-9-Octadecenoic Acid, 1-[[(1-oxooctadecyl)oxy]methyl]-2-(phosphonooxy)ethyl Ester.*
SOPA [R.N. 10016-26-9; see also 20337-09-1]: Spectra: FAB-MS.[1369] Chromatography: HPLC.[2108]

1-Stearoyl-2-linoleoyl-*sn*-glycero-3-(dihydrogen phosphate) (SLPA), 18:0/18:2 PA, $C_{39}H_{73}O_8P$. *[R-(Z,Z)]-9,12-Octadecadienoic Acid, 1-[[(1-oxooctadecyl)oxy]methyl]-2-(phosphonooxy)ethyl Ester.*
SLPA [R.N. 120661-82-7]: Chromatography: HPLC.[2108]

1,2-Dioleoyl-*sn*-glycero-3-(dihydrogen phosphate) (DOPA), 18:1/18:1 PA, $C_{39}H_{73}O_8P$. *[R-(Z,Z)]-9-Octadecenoic Acid, 1-[(Phosphonooxy)methyl]-1,2-Ethanediyl Ester.*
DOPA [R.N. 61617-08-1]: Viscous oil, highly soluble in chloroform, ethanol, acetone, ether, petroleum ether, and benzene, insoluble in water; $[\alpha]_D$ +3.8° ($CHCl_3$)[2409]; DSC.[2328] Spectra: $^1H$ NMR,[2379] $^2H$ and $^{31}P$ NMR (figs.),[2328] FAB-MS.[1369] Chromatography: TLC,[2379] IEC,[2285] HPLC.[2103]
$NaC_{39}H_{72}O_8P$: Waxlike material, highly soluble in ether and chloroform, slightly soluble (0.6 g/100 mL) in ethanol; $[\alpha]_D^{24}$ +3.3° ($CHCl_3$).[2409]
$(NH_4)_2C_{39}H_{71}O_8P$: Solid.[2285]

1,2-Dilinoleoyl-*sn*-glycero-3-(dihydrogen phosphate) (DLPA), 18:2/18:2 PA, $C_{39}H_{69}O_8P$. *[R-(all Z)]-9,12-Octadecadienoic Acid, 1-[(Phosphonooxy)methyl]-1,2-Ethanediyl Ester.*

DLPA [R.N. 17966-17-5]: Chromatography: HPLC.[2103]

1-Linoleoyl-2-linolenoyl-*sn*-glycero-3-(dihydrogen phosphate) (LLnPA), 18:2/18:3 PA, $C_{39}H_{67}O_8P$. *[R-(all Z)]-9,12,15-Octadecatrienoic Acid, 1-[[(1-oxo-9,12-octadecadienyl)oxy]-methyl]-2-(phosphonooxy)ethyl Ester.*

LLnPA [R.N. 228874-67-3; see also 142010-42-2]: Chromatography: HPLC.[2100]

1,2-Dilinolenoyl-*sn*-glycero-3-(dihydrogen phosphate) (DLnPA), 18:3/18:3 PA, $C_{39}H_{65}O_8P$. *[R-(all Z)]-9,12,15-Octadecatrienoic Acid, 1-[(Phosphonooxy)methyl]-1,2-Ethanediyl Ester.*

DLnPA [R.N. 34961-23-4; see also 94086-57-4]: Oil, $[\alpha]_D^{20}$ +3.1° ($CHCl_3$).[2292] Chromatography: TLC,[2292] HPLC.[2100]

## Synthesis

DPPA may be prepared (a) by phosphorylation of 1,2-dipalmitoyl-*sn*-glycerol with diphenyl phosphorochloridate,[2397] *o*-phenylene phosphorochloridate,[2399] $POCl_3$,[2410] bis(2,2,2-trichloroethyl)phosphorochloridate,[2285] or 1,2-dibromo-1-phenylethanephosphonic acid[2396] in the presence of a tertiary amine, (b) by condensation of 1,2-dipalmitoyl-*sn*-glycero-3-iodohydrin with silver dibenzyl phosphate,[2411] (c) by acylation of *sn*-glycero-3-phosphate or one of its derivatives with palmitoyl chloride[2412] or palmitic anhydride,[2404,2413] or (d) by enzymatic hydrolysis of DPPC with phospholipase D.[2395] POPA may be prepared (a) by phosphorylation of 1-palmitoyl-2-oleoyl-*sn*-glycerol with bis(2,2,2-trichloroethyl) phosphorochloridate[2407] or (b) by enzymatic hydrolysis of POPC with phospholipase D.[2414] PLPA may be prepared by condensation of 1-palmitoyl-2-linoleoyl-*sn*-glycero-3-iodohydrin with silver di(*p*-methylbenzyl) phosphate.[2298] DOPA may be prepared (a) by phosphorylation of 1,2-dioleoyl-*sn*-glycerol with bis(2,2,2-trichloroethyl) phosphorochloridate[2379] or $POCl_3$,[2409] (b) by acylation of *sn*-glycero-3-phosphate with oleic anhydride[2415] or (c) by enzymatic hydrolysis of DOPC with phospholipase D.[2379] DLPA may be prepared by phosphorylation of 1,2-dilinoleoyl-*sn*-glycerol with $POCl_3$.[2416] DLnPA may be prepared (a) by phosphorylation of 1,2-dilinolenoyl-*sn*-glycerol with $POCl_3$[2292] or (b) by enzymatic hydrolysis of DLnPC with phospholipase D.[2417]

## Hydrolysis

Hydrolysis of *DL*-DPPA with 0.1*N* NaOH in ethanol (3 h at reflux) gives *rac*-glycerol-3-phosphate with no migration or loss of phosphate.[2418]

# Lysophosphatidic Acids

## Physical Properties

1-Palmitoyl-*sn*-glycero-3-(dihydrogen phosphate) (PHPA), 16:0 PA, $C_{19}H_{39}O_7P$. *(R)-Hexadecanoic Acid, 2-Hydroxy-3-(phosphonooxy)propyl Ester.*

PHPA [R.N. 7220-34-0]: Colorless solid.[2419] Spectra: EI-MS and CI-MS (figs.).[2420] Chromatography: TLC,[2421] AgTLC,[2422] HPLC,[2422] GFC.[2420]

$NaC_{19}H_{38}O_7P$ [R.N. 17618-08-5]: Colorless powder, $[\alpha]_D^{20}$ +13.2° ($CHCl_3$), IR, PC.[2419]
2-Palmitoyl-*sn*-glycero-3-(dihydrogen phosphate) (HPPA), 16:0 PA, $C_{19}H_{39}O_7P$. *(R)-Hexadecanoic Acid, 1-Hydroxy-3-(phosphonooxy)propyl Ester.*
HPPA: Chromatography: TLC,[2421] AgTLC.[2422]

1-Stearoyl-*sn*-glycero-3-(dihydrogen phosphate) (SHPA), 18:0 PA, $C_{21}H_{43}O_7P$. *(R)-Octadecanoic Acid, 2-Hydroxy-3-(phosphonooxy)propyl Ester.*
SHPA [R.N. 65494-37-3]: Spectra: EI-MS and CI-MS.[2420] Chromatography: GFC,[2420] HPLC,[2422] AgTLC.[2422] *rac-SHPA* [R.N. 19491-32-8]: mp 85-87 °C, TLC.[2423]

2-Stearoyl-*sn*-glycero-3-(dihydrogen phosphate) (HSPA), 18:0 PA, $C_{21}H_{43}O_7P$. *(R)-Octadecanoic Acid, 1-Hydroxy-3-(phosphonooxy)propyl Ester.*
HSPA: No data. For *rac-HSPA*: Colorless crystals, mp 74.5-75.5 °C, IR (fig.), TLC.[2423]

1-Oleoyl-*sn*-glycero-3-(dihydrogen phosphate) (OHPA), 18:1 PA, $C_{21}H_{41}O_7P$. *[R-(Z)]-9-Octadecenoic Acid, 2-Hydroxy-3-(phosphonooxy)propyl Ester.*
OHPA [R.N. 6552-98-5]: Chromatography: TLC,[2421] AgTLC,[2422] HPLC.[2422]

2-Oleoyl-*sn*-glycero-3-(dihydrogen phosphate) (HOPA), 18:1 PA, $C_{21}H_{41}O_7P$. *[R-(Z)]-9-Octadecenoic Acid, 1-Hydroxy-3-(phosphonooxy)propyl Ester.*
HOPA: Chromatography: TLC,[2421] AgTLC.[2422]

1-Linoleoyl-*sn*-glycero-3-(dihydrogen phosphate) (LHPA), 18:2 PA, $C_{21}H_{39}O_7P$. *[R-(Z,Z)]-9,12-Octadecadienoic Acid, 2-Hydroxy-3-(phosphonooxy)propyl Ester.*
LHPA [R.N. 65528-85-0]: Chromatography: AgTLC, HPLC.[2422]

1-Linolenoyl-*sn*-glycero-3-(dihydrogen phosphate) (LnHPA), 18:3 PA, $C_{21}H_{37}O_7P$. *[R-(Z,Z,Z)]-9,12,15-Octadecatrienoic Acid, 2-Hydroxy-3-(phosphonooxy)propyl Ester.*
LnHPA [R.N. 68041-32-7]: Chromatography: AgTLC, HPLC.[2422]

## Synthesis

PHPA may be prepared by the phosphorylation of 2-benzyl-1-palmitoyl-*sn*-glycerol with $POCl_3$[2419] or of 1-palmitoyl-*sn*-glycerol with ATP in the presence of DG kinase,[2421] or (b) by hydrolysis of DPPA with snake venom phospholipase $A_2$.[2424] HPPA may be prepared by phosphorylation of 2-palmitoyl-*sn*-glycerol with ATP in the presence of DG kinase.[2421] SHPA may be prepared (a) by phosphorylation of 1-stearoyl-*sn*-glycerol with ATP in the presence of DG kinase[2422] or (b) by enzymatic hydrolysis of SHPC with phospholipase D.[2420] OHPA may be prepared (a) by phosphorylation of 1-oleoyl-*sn*-glycerol with $PCl_3$/$H_3PO_4$[2425] or with ATP in the presence of DG kinase[2421] or (b) by enzymatic hydrolysis of DOPA with snake venom phospholipase $A_2$.[2424] HOPA may be prepared by phosphorylation of 2-oleoyl-*sn*-glycerol with ATP in the presence of DG kinase.[2421] LHPA may be prepared by phosphorylation of 1-linoleoyl-*sn*-glycerol with ATP in the presence of DG kinase.[2422] LnHPA may be prepared by phosphorylation of 1-linolenoyl-*sn*-glycerol with ATP in the presence of DG kinase (Table 4-15).[2422]

**Table 4-15** Phospholipids in Plants*

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Abelmoschus esculentus* (L.) Moench (Okra) | | | | | | | | | | | |
| 2 | Seed | TLC | + | + | | + | + | | | 0.62-0.68 | 1426 |
| 5 | Seed | TLC | 48.4-52.4 | 17.7-20.5 | | 24.0-26.2 | | 3.8-5.2 | | 19.3-21.9[a] | 1427 |
| 1 | Cotyledon | TLC | | | | NAPE + | | | | | 1361 |
| *Acacia arabica* (Lam.) Willd. (Gum Arabic Tree) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | (LPC +) | | | | | 1428 |
| *Acacia catechu* (L.f.) Willd. (Catechu) | | | | | | | | | | | |
| 1 | Seed | TLC | 36.0 | 25.8 | 7.4 | 21.8 | | | 9.0 | 0.35[c] | 1429 |
| *Acer platanoides* L. (Norway Maple) | | | | | | | | | | | |
| 1 | Seed | TLC | 53.0 | 20.8 | | 14.8 | | 11.5 | | 2.3[c,v] | 1430 |
| 1 | Seed[k] | TLC | 179 | 60 | 22 | 49 | | 12 | | | 1431 |
| *Acer pseudoplatanus* L. (Sycamore Maple) | | | | | | | | | | | |
| 1 | Seed[k] | TLC | 164 | 48 | 19 | 41 | 6 | | | | 1431 |
| 1 | Cell culture | TLC | 47 | 29 | 5 | 16 | | | 1.8 | 160[j] | 1432 |
| 1 | –, mitochondria | TLC | 43 | 35 | 3 | 6 | | | 13 | 300[j] | 1432 |
| 1 | –, inner membrane | TLC | 41 | 37 | 2.5 | 5 | | | 14.5 | 400[j] | 1432 |
| 1 | –, outer membrane | TLC | 54 | 30 | 4.5 | 11 | | | 0 | 830[j] | 1432 |
| 1 | –, amyloplast envelope membrane | TLC | 59 | 1 | 25 | 15 | | | | | 1433 |
| 1 | –, tonoplast | TLC | 30.3 | 46.7 | 2.3 | 15.3 | 2.5 | 1.4 | (LPC 1.6) | 44.5[a] | 1434 |
| *Adansonia digitata* L. (Baobab) | | | | | | | | | | | |
| 1 | Seed, shelled | Frac. pptn. | 37 | 63 | | 0 | | | | 0.13 | 1435 |
| *Adiantum hispidulum* Swarz. (Australian Maidenhair Fern) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Aegilops speltoides* Tausch. (Goatgrass) | | | | | | | | | | | |
| 2 | Leaf, chloroplast[m] | TLC | 0.07-0.09 | | 0.22-0.27 | | | | | | 1437 |
| *Aegilops squarrosa* L. (Barb Goatgrass) | | | | | | | | | | | |
| 2 | Leaf, chloroplast[m] | TLC | 0.05-0.09 | | 0.27 | | | | | | 1437 |
| *Aegopodium podagraria* L. (Goutweed) | | | | | | | | | | | |
| 1 | Seed | TLC | 47 | 19 | Trace | 14 | | 20 | | 0.6[a] | 1438 |
| | | | also LPC trace, LPE trace. | | | | | | | | |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]µmol PL/mg protein; [i]µmol PL/mg chlorophyll; [j]µg PL/mg protein; [k]µg lipid P/g; [l]µmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]µmol PL/g dwb; [p]µg PL/100 mg fwb; [q]µg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]µmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]µg PL/mL; [x]µg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]µg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]µg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Aesculus hippocastanum* L. (European Horse Chestnut) | | | | | | | | | | | |
| 1 | Leaf, thylakoid[a] | TLC | | | 12.4 | | | | | | 1439 |
| *Agathis robusta* Bailey (Queensland Kauri) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | | | | | | | 1436 |
| *Agave americana* L. (Maguey) | | | | | | | | | | | |
| 1 | Leaf | TLC | | | 7 | | | | | | 1440 |
| *Agave miradorensis* Jacobi (Dwarf Century Plant) | | | | | | | | | | | |
| 1 | Leaf | TLC | | | 7 | | | | | | 1440 |
| *Agave sisalana* Perrine (Sisal Hemp) | | | | | | | | | | | |
| 1 | Leaf | TLC | | | 8 | | | | | | 1440 |
| *Alchemilla pentaphylla* L. (Lady's Mantle) | | | | | | | | | | | |
| 1 | Leaf | TLC | 51 | 20 | 17 | 10 | | | 1 | 0.40 | 1441 |
| *Aleurites montana* (Lour.) E. H. Wils. (Chinese Tung) | | | | | | | | | | | |
| 1 | Seed | TLC | 25.5 | 6.6 | 34.7 | 28.6 | | | 4.6 | 1.9[a] | 1442 |
| 1 | Leaf | TLC | 50.0 | 21.2 | 17.1 | 7.0 | Trace | | 4.7 | 17.0[a] | 1443 |
| *Alhagi persarum* Boiss. (Camel's Thorn) | | | | | | | | | | | |
| 1 | Seed[aa] | TLC | + | + | + | + | (NAPE +, NALPE +) | | | 1.5 | 1444 |
| *Alhagi pseudalhagi* (M. Bieb.) Desv. | | | | | | | | | | | |
| 1 | Seed[aa] | TLC | + | + | + | + | | + | | 1.1 | 1444 |
| | | | also NAPE +, LPC +. | | | | | | | | |
| *Alisma plantago-aquatica* L. (Mad Dog Weed) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 55.8 | 13.2 | 16.4 | 9.7 | 1.7 | 2.8 | | 1.49[c] | 1445 |
| *Allium ascalonicum* L. (Scallion) | | | | | | | | | | | |
| 1 | Leaf | TLC | 25.3 | 59.0 | 1.2 | | | 8.5 | 6.0 | 0.254 | 1446 |
| *Allium cepa* L. (Onion) | | | | | | | | | | | |
| 1 | Seed | TLC | 50.8 | 24.2 | | 16.9 | | 8.1 | | 1.24[l] | 1447 |
| 1 | Root | TLC | 19.4 | 21.2 | 18.8 | 10.6 | 8.1 | 13.1 | 8.8 | 16.6[e] | 1448 |
| 1 | Root tip, total particulates | TLC | 54.0 | 21.6 | 6.1 | 7.1 | 2.4 | 2.5 | 5.2 | | 1449 |
| | | | also LPC 0.8, LPE 0.2 | | | | | | | | |
| 1 | –, nuclei | TLC | 27.1 | 20.4 | 5.6 | 8.0 | 3.1 | 24.6 | 1.2 | 1.2 | 1449 |
| | | | also LPC 5.2, LPE 4.9 | | | | | | | | |
| 1 | –, nuclear membrane | TLC | 52.2 | 25.8 | 5.2 | 7.3 | 0 | 4.5 | 1.8 | 6.9 | 1449 |
| | | | also LPC 1.4, LPE 1.9 | | | | | | | | |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, crude microsome | TLC | 19.2 | 19.3 | 5.2 | 7.9 | 4.3 | 31.6 | 1.6 | 9.2 | 1449 |
| | | | also LPC 5.8, LPE 5.3 | | | | | | | | |
| 1 | –, rough microsome | TLC | 50.3 | 26.6 | 5.2 | 5.9 | 2.4 | 4.6 | 1.2 | 13.7 | 1449 |
| | | | also LPC 1.5, LPE 2.1 | | | | | | | | |
| *Allium fistulosum* L. (Welsh Onion) | | | | | | | | | | | |
| 1 | Leaf | TLC | | | | | + | | | | 1450 |
| *Allium porrum* L. (Leek) | | | | | | | | | | | |
| 2 | Leaf (1) | TLC | 34.4 | 7.5 | 15.6 | | | 10.5 | 32.0 | 0.818 | 1446 |
| | Leaf (2) | TLC | 43.2 | 9.5 | 14.8 | | | 11.3 | 21.2 | 0.738 | 1446 |
| 1 | Leaf[l] | Choline | 30 | | | | | | | | 1451 |
| 1 | 7-day seedling, endoplastic reticulum | TLC | 75.9 | 19.2 | | 3.2 | 1.7 | | | | 1452 |
| *Allium sativum* L. (Garlic) | | | | | | | | | | | |
| 1 | Leaf | TLC | 15.2 | 35.1 | 16.4 | | | 16.6 | 15.8 | 0.136 | 1446 |
| 2 | Clove *incl. PS | TLC | 60.0-61.0* | 25.0-25.3 | 10.1-11.4 | | | 3.6 | | 0.112-0.134 | 1453 |
| *Allium turcomanicum* Regel | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 1.1 | 794 |
| *Alnus rubra* Bong. Red Alder | | | | | | | | | | | |
| 1 | Root | HPLC | + | + | | + | | | | | 1454 |
| 1 | –, nodule | HPLC | + | + | | + | | | | | 1454 |
| *Alocasia macrorrhiza* (L.) G. Don (Giant Taro) | | | | | | | | | | | |
| 1 | Tuber, peeled | TLC | 41.5 | 29.3 | | 14.6 | | | | 0.12[c] | 1455 |
| *Aloe vera* (L.) Burm. f. (Curaçao Aloe) | | | | | | | | | | | |
| 1 | Overground pieces | TLC | 12.0 | 12.0 | | 2.7 | 6.5 | 47.3 | (LPI 1.2) | 0.92 | 1456 |
| *Althaea rosea* (L.) Cav. (Hollyhock) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | + | + | + | + | + | 1.3 | 1457 |
| | | | also LPC +, LPE +, NALPE + | | | | | | | | |
| *Amaranthus arthropurpureus* | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | + | | | | | 1458 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]µmol PL/mg protein; [i]µmol PL/mg chlorophyll; [j]µg PL/mg protein; [k]µg lipid P/g; [l]µmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]µmol PL/g dwb; [p]µg PL/100 mg fwb; [q]µg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]µmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]µg PL/mL; [x]µg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]µg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]µg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Amaranthus blitus* L. (Wild Blite) | | | | | | | | | | | |
| 1 | Leaf | CC (silica) | 13.1 | | | | | | | 2.40[l] | 1459 |
| *Amaranthus cruentus* L. (Purple Amaranth) | | | | | | | | | | | |
| 1 | Seed | TLC | 26 also LPC 8, LPE 2 | 16 | 6 | 10 | 0 | | 8 | 5.0[a] | 1460 |
| 1 | Seed | TLC | + | + | | | + | | | | 1461 |
| 1 | Leaf[i] | TLC | 0.92 | 0.38 | 0.49 | | | | | | 1462 |
| 1 | –, chloroplast[i] | TLC | 0.05 | 0 | 0.30 | | | | | | 1462 |
| 1 | –, bundle-sheath strand[i] | TLC | 0.29 | 0.10 | 0.42 | | | | | | 1462 |
| 1 | Callus culture[k] | TLC | | | | 960 | | | | | 1463 |
| *Amaranthus deflexus* L. | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.96 | | | | | | 1402 |
| *Amaranthus hybridus* L. (Green Amaranth) | | | | | | | | | | | |
| 1 | Seed | TLC | 50 | 33 | | 17 | | | | 0.40 | 1458 |
| *Amaranthus hypochondriacus* L. (Prince's Feather) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | | + | | | | 1461 |
| *Amaranthus lividus* Willd (Wild Blite) | | | | | | | | | | | |
| 1 | Leaf, chloroplast | TLC | | | + | | | | | | 1402 |
| *Amaranthus powellii* S. Wats. (Powell Amaranth) | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 1.14 | | | | | | 1402 |
| *Amaranthus retroflexus* L. (Redroot Pigweed) | | | | | | | | | | | |
| 1 | Leaf, thylakoid | TLC | 35 | | 56 | 8 | | | | 1987[q] | 1464 |
| 1 | Leaf, chloroplast | HPLC | 44.8 | 35.4 | 11.2 | 8.5 | | | | 78.0[a] | 1465 |
| *Amaranthus spinosus* L. (Spiny Amaranth) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | + | | | | | 1458 |
| *Amaranthus tricolor* L. (Tampala) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | + | | | | | 1458 |
| 1 | Leaf | TLC | 21 | 25 | 25 | 13 | | | 16 | 1.33[c] | 1466 |
| *Amaryllis* spp. (Amaryllis) | | | | | | | | | | | |
| 1 | Leaf | TLC | | | 10 | | | | | | 1440 |
| *Amorpha fruticosa* L. (Dull Leaf Indigobush) | | | | | | | | | | | |
| 1 | Seed[s] | | + | | | | | | | | 1467 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Anacardium occidentale* L. (Cashew) | | | | | | | | | | | |
| 1 | Seed kernel | TLC | 11.6 | 11.0 | | (LPC 7.0) | | 7.5 | 4.6 | 0.95 | 1468 |
| 1 | Nut kernel | TLC | 53.6 | 14.0 | + | | 6.5 | (LPC 5.1) | | | 1469 |
| 1 | Fruit, juice | TLC | + | + | + | | | (LPC +) | | | 1469 |
| *Androsace helvetica* (L.) All. (Swiss Rock Jasmine) | | | | | | | | | | | |
| 1 | Leaf | TLC | 58 | 20 | 10 | 10 | | | 3 | 0.16 | 1441 |
| *Anethum graveolens* L. (Dill) | | | | | | | | | | | |
| 1 | Leaf | TLC | 39.4 | 1.3 | 55.4 | 0.9 | | | 3.0 | 1.64[c] | 1470 |
| 1 | Stem | TLC | 69.3 | 3.5 | 25.4 | 0 | | | 1.8 | 0.55[c] | 1470 |
| 1 | Fruit | TLC | 43.0 | 17.9 | | 20.5 | | 8.6 | | 0.2 | 1471 |
| | | | also LPC 4.2, LPE 1.9 | | | | | | | | |
| *Angelica sinensis* (Olivi) Diels (Danggui) | | | | | | | | | | | |
| 3 | Leaf? | TLC | 35.5-61.0 | 13.7-28.7 | | 0.1-2.4 | 0.1-2.0 | 0.3-4.3 | 10.9-30.6 | | 1472 |
| *Anomodon viticulosus* (Hedw.) Hook. and Taylor (Anomodon Moss) | | | | | | | | | | | |
| 1 | Whole plant *incl. LPE | TLC | 76.7 | 8.4 | 7.6 | 4.5* | 2.8 | | | 0.35[c] | 1473 |
| *Anthoceros laevis* (L.) var. *lorbeer* | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Anthriscus cerefolium* L. (Chervil) | | | | | | | | | | | |
| 1 | Seed | TLC | 28 | 7 | 3 | 42 | | 17 | 2 | 1.0[a] | 1438 |
| *Antirrhinum majus* L. (Snapdragon) | | | | | | | | | | | |
| 1 | Leaf, chloroplast | TLC | 5.7 | | 87.7 | 6.6 | | | | 2.11[c] | 1408 |
| 1 | –, thylakoid membr. | TLC | 5.5 | | 80.4 | 14.1 | | | | 1.99[c] | 1408 |
| *Apium graveolens* L. ssp. *dulce* (Celery) | | | | | | | | | | | |
| 1 | Seed | TLC | Trace | 33 | | 33 | | (LPE 33) | | 0.78 | 1474 |
| 1 | Leaf | TLC | 17.4 | 44.4 | 32.7 | | | 1.6 | 3.9 | 0.792 | 1446 |
| 1 | Stem | TLC | 37.3 | 35.8 | 5.4 | | | 8.7 | 12.8 | 0.795 | 1446 |
| 1 | Fruit | TLC | 40.6 | 14.1 | | 29.1 | | 7.1 | | 0.4 | 1471 |
| | | | also LPC, 3.0, LPE 3.1 | | | | | | | | |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]µmol PL/mg protein; [i]µmol PL/mg chlorophyll; [j]µg PL/mg protein; [k]µg lipid P/g; [l]µmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]µmol PL/g dwb; [p]µg PL/100 mg fwb; [q]µg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]µmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]µg PL/mL; [x]µg lipid P/cm$^2$ leaf area; [y]Molecules per 10$^6$ plastids; [z]µg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]µg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Cell culture | TLC | 29.9 | 15.4 | | | | | | 24.1[o] | 1475 |
| *Apodanthera undulata* Gray (Melon-Loco) | | | | | | | | | | | |
| 1 | Seed | TLC | 68.5 | 13.3 | | 13.7 | | (LPC 4.5) | | 4.0[a] | 1476 |
| *Arabidopsis thaliana* (L.) Heynh (Mouse-Ear Cress) | | | | | | | | | | | |
| 1 | Leaf | TLC | 41.8 | 25.1 | 24.6 | 8.5 | | | | | 1477 |
| 1 | Leaf, plasma membrane | TLC | 35.5 | 38.9 | 9.0 | 10.3 (incl. PS) | | 6.4 | | 46.8[a] | 1478 |
| 1 | Leaf, protoplast | TLC | 27.9 | 21.8 | 23.6 | | | | 26.7 | | 1479 |
| *Arachis hypogaea* L. (Peanut) | | | | | | | | | | | |
| 1 | Nut | TLC | 21.0 | 18.0 | 6.5 | 9.0 | | 10.0 | | 1.2[a] | 1480 |
| 1 | Nut[n] | TLC | 2.7 | 0.5 | | 1.5 | 0 | (Phyto GP 0.9) | | | 1481 |
| 1 | Nut, oil body | TLC | 61.6 | 5.0 | | 8.4 | 25.0 | | | 0.80 | 1482 |
| 1 | Seed | HPLC | 51.2 | 16.8 | 2.0 | | | 1.6 | 17.4 | 1.3[a] | 1483 |
| 1 | Leaf | TLC | 32.8 | 20.6 | 16.1 | 13.7 | | | 16.8 | 6.1[l] | 1484 |
| 1 | –, chloroplast | TLC | 33.7 | | 39.1 | 27.2 | | | | 191.9[q] | 1485 |
| 1 | –, hypocotyl | TLC | 32.4 | 27.0 | 17.6 | 23.0 | | | | 0.017 | 1486 |
| *Araucaria cunninghamii* Ait. (Moreton Bay Pine) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | | | | | | | 1436 |
| *Araucaria heterophylla* (Salisb.) Franco (Norfolk Pine) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | | | | | | | 1436 |
| *Aronia melanocarpa* L. (Chokeberry) | | | | | | | | | | | |
| 1 | Seed[e] | TLC | 19.9 also LPC 10.8, LPE 1.4 | 16.6 | 0.8 | 29.8 | 0 | 15.8 | 2.0 | | 1487 |
| *Arthrocnemum indicum* (Willd.) Moq. | | | | | | | | | | | |
| 1 | Shoot | TLC | 36.3 | 6.2 | 18.6 | 5.8 | | 4.0 | 26.5 | 0.226[c] | 1488 |
| *Arum maculatum* L. (Cuckoopint) | | | | | | | | | | | |
| 1 | Leaf, chloroplast[a] | TLC | | | 9 | | | | | | 1489 |
| 1 | Spadix, mitochondria | TLC | 20.0 | 33.0 | 6.6 | 6.9 | 1.5 | 2.6 | 11.0 | | 1490 |
| *Asplenium viride* Huds. (Green Spleenwort) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Astragalus chinensis* L. (Chinese Milk Vetch) | | | | | | | | | | | |
| 1 | Seed[c] | TLC | 0.204 | | | | | | | | 1491 |
| *Atrichum angustatum* (Brid.) Bryol. eur. | | | | | | | | | | | |
| 1 | Whole plant *incl. LPE | TLC | 28.2 | 21.8 | 25.2 | 12.5* | 7.7 | | | 1.69[c] | 1492 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Atrichum haussknechtii* Jur. et Milde | | | | | | | | | | | |
| 1 | Whole plant | TLC | 39.5 | 14.8 | 15.2 | 10.3 | 11.0 | | | 1.17[c] | 1493 |
| *Atriplex gmelinic* C.A. Mey | | | | | | | | | | | |
| 1 | Leaf | TLC | 52.2 | 7.5 | 7.5 | | | | | 2.84[c] | 1494 |
| 1 | Root | TLC | 60.4 | 30.8 | Trace | | | | | 0.38[c] | 1494 |
| *Atriplex prostrata* DC | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.60 | | | | | | 1402 |
| *Atropa belladonna* L. (Belladonna) | | | | | | | | | | | |
| 1 | Cell culture | TLC | 51.1 | 28.1 | 7.8 | 9.6 | | Trace | | 0.65[e] | 1495 |
| *Aulacomnium palustris* (Hedw.) Schwägr. | | | | | | | | | | | |
| 1 | Whole plant | TLC | 49.5 | 20.9 | 17.4 | 5.2 | 7.2 | | | 0.26[c] | 1493 |
| *Avena sativa* L. (Oats) | | | | | | | | | | | |
| 1 | Seed, dehulled *Incl. PA | TLC | 29.9 | 14.8 | 9.5 | 3.9* | 3.2 | (LPC,LPE,LPS 20.4) | | 1.55[c] | 1496 |
| 1 | Seed | TLC | | NAPE 0.41 mg/seed | | | | | | | 1497 |
| 1 | Seed | PC | | NAPE +, NALPE + | | | | | | | 1498 |
| 1 | Starch | TLC | | LPC 51.6, LPE 5.1, LPI 7.0 | | | | | | 1.3 | 1499 |
| 1 | Starch | TLC | LPC 67.4, LPE 7.8, LPG 12.0, LPI trace, LPS trace | | | | | | | 1.25 | 1500 |
| 1 | Coleoptile plasma membrane | TLC | 23.0 | 21.6 | 4.3 | 5.5 | 7.7 | 35.5 | (LPC 2.4) | 0.55[h] | 1501 |
| 1 | Leaf | TLC | | | | | + | | | | 1450 |
| 1 | Leaf, plasma membrane | TLC | 35.1 | 29.2 | 6.6 | 9.4 (incl. PS) | | 15.3 | | 28.8[a] | 1502 |
| 1 | –, mitochondria | TLC | 40.7 | 33.3 | 8.4 | 3.4 | | | 14.1 | | 1503 |
| 1 | –, chloroplast | TLC | 30.9 | 61.4 | 7.7 | | | | | | 1503 |
| 1 | Stem, internode | TLC | 50 | 31 | 8 | 6 | 5 | | | 2.15[c] | 1504 |
| 1 | –, node | TLC | 43 | 35 | 7 | 9 | 5 | | | 0.76[c] | 1504 |
| 1 | –, leaf sheath | TLC | 31 | 46 | 14 | 3 | 6 | | | 0.35[c] | 1504 |
| 1 | Shoot, plasma membrane[j] | HPLC | 77.3 | 70.3 | | | | | | | 1505 |
| 1 | Root, whole[g] | Choline | 0.54 | | | | | | | 1.37 | 1386 |
| 1 | –, cell wall[g] | Choline | 0.021 | | | | | | | 0.027 | 1506 |
| 1 | –, mitochondria[g] | Choline | 0.031 | | | | | | | 0.045 | 1506 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, mictosomes[g] | Choline | 0.319 | | | | | | | 0.555 | 1506 |
| 1 | Root, plasma membrane | TLC | 18.2 | 10.5 | 4.0 | 3.7 | | 13.9 | | 0.33[c] | 1507 |
| | | | also LPC 4.9, LPE 6.3 | | | | | | | | |
| 1 | –, mitochondria | TLC | 9.9 | 6.5 | 4.2 | 3.0 | | 41.3 | 9.3* | 0.19[c] | 1507 |
| | | | also LPC 8.9, LPE 5.4 | | | | | | *Incl. glycolipid | | |
| 1 | Root, plasmalemma[n] | TLC | 18 | 36 | | + | + | | | | 1508 |
| 1 | –, microsomes[n] | TLC | 29 | 27 | | + | + | | | | 1508 |
| *Avicennia germinans* (L.) L. (Black Mangrove) | | | | | | | | | | | |
| 1 | Root | TLC | 35.7 | 28.9 | | 10.7 | | | | 32[k] | 1509 |
| *Avicennia resinifera* Forst. | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.46 | | | | | | 1402 |
| *Azolla filiculoides* Lam. (Pacific Mosquitofern) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Balanites aegyptiaca* (L.) Del. (Desert Date) | | | | | | | | | | | |
| 1 | Seed, kernel | TLC | + | + | | + | | + | | | 1510 |
| *Barbarea verna* (Mill) Aschers (Winter Cress) | | | | | | | | | | | |
| 1 | Seed oil | TLC | 35 | 25 | | 5 | 10 | 10 | 10 | | 1511 |
| *Bartramia halleriana* Hedw. (Haller's Bartramia Moss) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Benincasa hispida* (Thunb.) Cogn. (Wax Gourd) | | | | | | | | | | | |
| 1 | Seed, ripe | TLC | + | + | | + | + | | | 0.10 | 1512 |
| 1 | –, unripe | TLC | + | + | | + | + | | | 0.26 | 1512 |
| *Beta cicla* L. (Swiss Chard) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | + | + | | | | | 1513 |
| *Beta maritima* L. (Sea Beet) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | + | + | | | | | 1513 |
| *Beta orientalis* Roth. | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | + | + | | | | | 1513 |
| *Beta patellaris* Moq. | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | + | + | | | | | 1513 |
| *Beta procumbens* C. Sm. | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | + | + | | | | | 1513 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Beta vulgaris* L., *crassa* group (Red Beet, Sugar Beet) | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | 0.404 | | | | | | | | 1514 |
| 1 | Leaf, stem | PC | 32.0 | 15.8 | 7.7 | 6.5 | 2.0 | 9.9 | 3.4 | 0.53 | 1515 |
| 1 | –, blade | PC | 36.4 | 12.3 | 17.0 | 6.5 | 2.0 | 4.0 | 4.0 | 1.03 | 1515 |
| 1 | –, chloroplast[a] | TLC | 2.5 | | 8.0 | | | | | | 1516 |
| 1 | Leaf | PC | 52 | 26 | 11 | 11 | | | | | 1517 |
| 1 | –, chloroplast | PC | 38 | 15 | 38 | 9 | | | | | 1517 |
| 2 | Root (1) | TLC | 19.5 | 3.4 | 31.2 | 6.4 | 4.9 | 21.6 | 10.6 | 0.081 | 1518 |
| | Root (2) | | 24.1 | 2.2 | 27.5 | 4.5 | 5.4 | 19.1 | 14.1 | 0.047 | |
| | | | also LPC 1.5, LPE 0.9 (1) and (2) LPC 1.9, LPE 1.2 (2) | | | | | | | | |
| 1 | Root | PC | 35.3 | 16.5 | 6.4 | 4.7 | 2.1 | 11.6 | 2.4 | 0.08 | 1515 |
| 1 | Root | Choline | 0.190 | | | | | | | 0.326 | 1519 |
| 1 | Root, vacuole | TLC | 54 | 24 | 4 | 5 | 1 | 12 | | 58[d] | 1520 |
| 1 | Root plasma membrane | TLC | 35.4 | 39.4 | 1.5 | | | 14.6 | | 1.3[h] | 1521 |
| *Betula pendula* Roth (Weeping Birch) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | + | + | + | | | 3.0[a] | 1522 |
| 1 | Bud | TLC | + | + | + | + | + | | | 1.1[a] | 1522 |
| *Bifora radians* M. Bieb. (Wild Bishop) | | | | | | | | | | | |
| 1 | Seed | TLC | 10 | 5 | 2 | 12 | 7 | 52 | 9 | 0.4[a] | 1438 |
| *Blechnum fluviatile* (R.Br.) Sal. (Ray Water Fern) | | | | | | | | | | | |
| 1 | Leaf | TLC | 35 | 18 | 26 | 6 | | | 15 | 2.28[l] | 1523 |
| *Blechnum spicant* (L.) Roth (Deer Fern) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Bougainvillea* spp. (Bougainvillea) | | | | | | | | | | | |
| 1 | Leaf | TLC | | | | | + | | | | 1450 |
| *Bouvardia ternifolia* (Cav.) Schl. (Firecracker Bush) | | | | | | | | | | | |
| 1 | Cell culture | TLC | 53.6 | 26.2 | 7.3 | 8.6 | | 0.5 | | 0.83[e] | 1495 |
| *Brachystegia nigera* Hoyle and Jones (Achi) | | | | | | | | | | | |
| 1 | Seed | TLC | 16 | 26 | 17 | 32 | | | 8 | 1.53[c] | 1524 |
| *Brachythecium* spp. | | | | | | | | | | | |
| 1 | Whole plant *Incl. LPE | TLC | 41.8 | 17.4 | 24.0 | 8.1* | 4.2 | | | 0.64[c] | 1492 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]µmol PL/mg protein; [i]µmol PL/mg chlorophyll; [j]µg PL/mg protein; [k]µg lipid P/g; [l]µmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]µmol PL/g dwb; [p]µg PL/100 mg fwb; [q]µg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]µmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]µg PL/mL; [x]µg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]µg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]µg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Brassica campestris* L. (Turnip Rape) | | | | | | | | | | | |
| 2 | Leaf, chloroplast | TLC | 3.0-4.8 | 1.6-1.8 | 7.8-8.0 | 1.6-3.4 (incl. SL) | | | 1.8-2.0 | 0.735-0.806[i] | 1525 |
| 1 | –, thylakoid | TLC | 35 | | 52 | 12 | | | | 1864[q] | 1464 |
| *Brassica campestris* L. ssp. *komatsuma* Mak. (Chinese Cabbage) | | | | | | | | | | | |
| 1 | Leaf | TLC | | | | | + | | | | 1450 |
| 1 | Leaf[l] | Choline | 0.2 | | | | | | | | 1451 |
| *Brassica campestris* L. ssp. *sarson* (Yellow Sarson) | | | | | | | | | | | |
| 1 | Seed | TLC | + also LPC + | + | + | + | + | + | + | | 1526 |
| *Brassica caulorapa* Pasq. (Kohlrabi) | | | | | | | | | | | |
| 1 | Stem | Fr. Prec. | 0.033 | | | | | | | | 1527 |
| 1 | Tuber[l] | Choline | 1 | | | | | | | | 1451 |
| *Brassica juncea* L. (Indian Mustard) | | | | | | | | | | | |
| 1 | Seed, oil body | TLC | 53.1 | 15.5 | | 13.1 | 18.3 | | | 1.60 | 1482 |
| *Brassica napus* L. (Rape) | | | | | | | | | | | |
| 3 | Seed | TLC | 20.0-30.0 also LPC 3.0-5.0, LPE 0-3.0, LPS 1.0-4.0, LPA 2.0-4.0 | 10.0-13.0 | | 2.0-10.0 | 19.0-21.0 | 10.0-15.0 | 5.0-11.0 | | 1528 |
| 2 | Seed (1) | TLC | 37.8 | 24.9 | 3.1 | 26.7 | | 3.7 | (LPC 3.8) | 630[k] | 1529 |
| | Seed (2) | TLC | 41.8 | 27.8 | 5.2 | 21.2 | | 1.8 | (LPC 2.2) | 630[k] | 1529 |
| 1 | Seed | TLC | 28.8 | 7.3 | 2.2 | 14.2 | | 41.6 | | | 1397 |
| 1 | Seed | HPLC | 25.6 | 12.8 | | 15.8 | | 44.8 | | | 1397 |
| 1 | Seed, oil body | TLC | 59.9 | 5.9 | | 14.0 | 20.2 | | | 1.97 | 1482 |
| 1 | Leaf[c] | TLC | 0.52 | 0.13 | 0.28 | 0.06 | | 0.05 | | | 1530 |
| 1 | Leaf | TLC | 20.8 | 26.3 | 20.1 | | | 11.3 | 20.1 | 0.431 | 1446 |
| 1 | –, thylakoid | TLC | 25 | | 44 | 32 | | | | 887[q] | 1464 |
| 1 | Root | TLC | 55 | 33 | | 7 | | | 5 | 26[o] | 1531 |
| 1 | Whole floret[a] | HPLC | 1.8 | 1.5 | | 0.5 | | 0.3 | (LPC 0.9, LPE 0.4) | | 1532 |
| 1 | –, elaioplast[a] | HPLC | 3.2 | 1.0 | | 0.2 | | 0.1 | (LPC 2.7, LPE 1.5) | | 1532 |
| 1 | –, tapetosome[a] | HPLC | 4.2 | 4.8 | | 1.1 | | 1.3 | (LPC 0.4, LPE 0.3) | | 1532 |
| 1 | Pollen, interior | HPLC | 50.6 | 35.0 | 2.6 | 10.0 | | 1.9 | | | 1533 |
| 1 | Pollen, coat | HPLC | 26.7 | 17.0 | 0 | 0 | | 56.3 | | | 1533 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Brassica napus* L. (Rape, low erucic acid (Canola)) | | | | | | | | | | | |
| 2 | Seed (1) | TLC | 41.2 | 23.7 | 6.8 | 26.2 | | 1.0 | (LPC 1.1) | 650[k] | 1529 |
| | Seed (2) | TLC | 53.8 | 19.2 | 4.8 | 14.8 | | 3.4 | (LPC 4.0) | 810[k] | 1529 |
| *Brassica napus* L. (Rape, low erucic acid, low glucosinolate (Double Zero Canola)) | | | | | | | | | | | |
| 2 | Seed (1) | TLC | 56.5 | 16.9 | 4.2 | 17.8 | | 2.0 | (LPC 2.6) | 430[k] | 1529 |
| | Seed (2) | TLC | 50.3 | 21.0 | 7.7 | 18.4 | | 1.5 | (LPC 1.1) | 740[k] | 1529 |
| *Brassica napus* L. var. *oleifera* (Winter Rape) | | | | | | | | | | | |
| 1 | Leaf[n] | HPLC | 1.8 | 2.4 | 2.5 | | | 2.7 | | | 1534 |
| 1 | Leaf | TLC | 31.5 | 18.2 | 26.3 | 9.6 | | 6.1 | | 1.60[c] | 1535 |
| 1 | Root | TLC | 38.2 | 40.4 | 4.6 | 7.9 | 1.7 | 3.1 | | 1.13[c] | 1535 |
| *Brassica nigra* (L.) Koch (Black Mustard) | | | | | | | | | | | |
| 1 | Seed | CC (silica) | 20.0 | 35.3 | | | | | | | 1536 |
| *Brassica oleracea* L. ssp. *acephala* DC (Kale) | | | | | | | | | | | |
| 1 | Leaf[f] | Choline | 18 | | | | | | | | 1451 |
| *Brassica oleracea* L. ssp. *botrytis* L. Cauliflower | | | | | | | | | | | |
| 1 | Bud, mitochondria | TLC | 44 | 34 | 4 | 7 | | | 11 | 356[j] | 1537 |
| 1 | Bud, inner membrane | TLC | 41 | 37 | 3 | 5 | | | 14 | 409[j] | 1537 |
| 1 | –, outer membrane | TLC | 42 | 24 | 10 | 21 | | | 3 | 634[j] | 1537 |
| 1 | –, microsomes | TLC | 50 | 35 | 8 | 6 | | | 1 | 510[j] | 1537 |
| 1 | –, plastid | TLC | 54 | 6 | 23 | 14 | | | 1.7 | | 1538 |
| 1 | –, plasma membrane | TLC | 38 | 15 | 4 | 8 | 7 | | 1 | | 1539 |
| | | | also LPC 4 and LPE 3. | | | | | | | | |
| 1 | –, plastid envelope membrane | TLC | 60 | 3 | 26 | 11 | | | | | 1433 |
| *Brassica oleracea* L. ssp. *capitata* L. (Cabbage) | | | | | | | | | | | |
| 3 | Leaf | TLC | 12.0-15.9 | 15.1-31.0 | 21.5-29.9 | 3.8-7.8 | 5.3-11.4 | 10.8-16.9 | 1.9-4.0 | 0.028-0.037 | 1540 |
| | | also LPC 0.9-2.1, LPE 1.4-3.0 | | | | | | | | | |
| 1 | Leaf | TLC | 20.8 | 25.0 | 26.6 | 7.8 | 3.9 | 9.1 | (NAPE 6.8) | 20.2[a] | 1541 |
| 1 | Leaf | CC | 29 | 27 | 6 | | 2 | | | | 1542 |
| 1 | Stalk | TLC | ++ | + | | | | + | | | 1396 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/cm$^2$ leaf area; [y]Molecules per 10$^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Brasica oleracea* ssp. *gemmifera* Zenk. (Brussels Sprouts) | | | | | | | | | | | |
| 1 | Leaf[l] | Choline | 21 | | | | | | | | 1451 |
| *Brassica rapa* L. ssp. *rapa* (Turnip) | | | | | | | | | | | |
| 1 | Seed | TLC | | $P_{NAPE}/P_{total} = 0.9$ | | | | | | | 1497 |
| 2 | Root | TLC | + | + | + | + | | + | + | | 1543 |
| *Bromus erectus* Huds. (Meadow Brome) | | | | | | | | | | | |
| 1 | Callus | TLC | 43 | 27 | 25 | | | 5 | | | 1544 |
| *Bryonia alba* L. (White Bryony) | | | | | | | | | | | |
| 1 | Root | TLC | 26.6 | 7.4 | 66.0 | | | | | | 1545 |
| *Bryum pseudotriquetrum* (Hedw.) Gärtn. *et al.* | | | | | | | | | | | |
| 1 | Whole plant | TLC | 11.2 | 31.9 | 20.7 | 10.6 | 13.4 | | | 1.17[c] | 1493 |
| *Buchanania lanzan* Spreng. (Almondette, Chironji) | | | | | | | | | | | |
| 1 | Seed, kernel | TLC | 23.0 | 47.0 | 12.0 | 10.0 | (LPC 3.0, LPE 5.0) | | | 4.06[c] | 1546 |
| *Buchloe dactyloides* Nutt. (Buffalograss) | | | | | | | | | | | |
| 1 | Root plasma membrane | TLC | 19.2 | 42.6 | 20.3 | 6.8 | 14.3 | | | 3.90[a] | 1547 |
| *Bupleurum rotundifolium* L. | | | | | | | | | | | |
| 1 | Seed | TLC | 23 | 8 | | 40 | | 25 | 4 | 1.4[a] | 1438 |
| | | | also LPC trace, LPE trace. | | | | | | | | |
| *Butea monosperma* (Lam.) Taub. (Palash) | | | | | | | | | | | |
| 1 | Seed, kernel | TLC | 44.6 | 14.8 | | 27.0 | | (LPC 4.9) | 1.8 | 0.84 | 1548 |
| *Butomus umbellatus* L. (Flowering Rush) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 53.3 | 25.5 | 10.4 | 5.6 | 1.4 | 3.7 | | 1.26[c] | 1445 |
| *Butyrospermum paradoxum* (Gaertn.f.) Hep. Shea Butter Tree | | | | | | | | | | | |
| 1 | Nut, kernel | TLC | 50 | 10 | | | 22 | | | 1.35[c] | 1549 |
| *Caesalpinia bonducella* (L.) Roxb. Sagargota | | | | | | | | | | | |
| 1 | Seed | TLC | 22.2 | 25.6 | | 30.6 | | | 19.8 | | 1550 |
| *Calendula officinalis* L. (Pot Marigold) | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 1.0 | 794 |
| *Calliergon cordifolium* (Hedw.) Kindb. | | | | | | | | | | | |
| 1 | Whole plant | TLC | 28.8 | 26.3 | 32.7 | 3.9 | 4.8 | | | 1.41[c] | 1551 |
| *Calocedrus formosana* Florin (Formosa Incense Cedar) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | | | | | | | 1436 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Caloncoba echinata* (Oliv.) Gilg. | | | | | | | | | | |
| 1 | Leaf | TLC | ++ | Trace | + | + | | Trace | | | 1552 |
| *Calophyllum inophyllum* L. (Alexandrian Laurel) | | | | | | | | | | |
| 1 | Seed, kernel | TLC | 33.8 | 46.3 | | | 6.1 | 8.1 | (LPC 5.7) | 0.96[c] | 1553 |
| *Calotropis gigantea* (L.) Ait.f. (Mudar) | | | | | | | | | | |
| 1 | Leaf | TLC | 32.5 | 15.7 | 22.0 | 14.1 | 4.7 | | 11.0 | 2.12[c] | 1554 |
| *Caltha palustris* L. (Cowslip) | | | | | | | | | | |
| 1 | Whole plant | TLC | 43.8 | 26.7 | 9.3 | 10.0 | 4.1 | | 3.4 | 6.97[c] | 1555 |
| *Camellia japonica* L. (Camellia) | | | | | | | | | | |
| 1 | Leaf | TLC | 43 | 19 | 14 | 4 | | | 19 | 4.65[l] | 1523 |
| *Camellia sinensis* L. (Tea) | | | | | | | | | | |
| 1 | Seed kernel[g] | TLC | 45 | 20 | 3 | 5 | | | | | 1556 |
| 1 | Young shoot[g] | TLC | 31 | 14 | 8 | 9 | | | | | 1556 |
| 1 | Coarse leaf[g] | TLC | 15 | 8 | 9 | 5 | | | | | 1556 |
| 1 | Leaf | TLC | 59.7 | 10.9 | 12.6 | 8.8 | | | 8.0 | 0.204 | 1557 |
| 1 | Pollen | TLC | 54 | 34 | 1 | 6 | | | | 1.30[c] | 1558 |
| *Canavalia ensiformis* (L.) DC (Jack Bean) | | | | | | | | | | |
| 1 | Root, nodule | TLC | 16 | 27 | 16 | 21 | 19 | | | 0.082 | 1559 |
| *Cannabis sativa* L. (Hemp) | | | | | | | | | | |
| 2 | Seed (1) | $^{31}$P NMR | 50.5 | 16.3 | | 25.5 | 0 | 3.4 | | 1.0[v] | 1560 |
| | Seed (2) | $^{31}$P NMR | 42.4 | 16.7 | | 27.2 | 0 | 7.4 | | 1.2[v] | 1560 |
| *Capparia spinosa* L. (Caper) | | | | | | | | | | |
| 1 | Plant, aerial parts | TLC | 16.6 | 20.4 | 26.1 | 12.8 | | 2.8 | | 8.0[a] | 1561 |
| | | | also NAPE 14.6, NALPE 6.7 | | | | | | | | |
| *Capsicum annuum* L. (Bell Pepper, Green Pepper) | | | | | | | | | | |
| 1 | Leaf[l] | TLC | 0.918 | | | | | | | | 1514 |
| 1 | –, chloroplast | TLC | 26.7 | 9.5 | 54.9 | 7.6 | | 1.3 | | 0.32[i] | 1562 |
| 1 | Fruit, whole | TLC | 75.8 | 8.7 | 2.3 | 4.1 | 2.1 | Trace | | 0.008 | 1563 |
| | | | also LPC 2.8, LPE trace | | | | | | | | |
| 1 | –, chloroplast | TLC | 33.7 | 24.8 | 24.7 | 12.4 | | 4.4 | | 0.0022[l] | 1564 |
| 1 | –, chromoplast | TLC | 58.6 | 11.4 | 14.3 | 14.8 | | 0.9 | | 0.0041[l] | 1564 |
| 1 | –, microsomal membr. | TLC | 58.1 | 28.5 | 1.8 | 10.4 | | 1.2 | | 0.036[l] | 1564 |
| 1 | Fruit, pericarp | TLC | 48.7 | 26.3 | 4.1 | 9.1 | | 8.8 | | 594[l] | 1565 |
| | | | also LPC (including LPE) 3.0 | | | | | | | | |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]µmol PL/mg protein; [i]µmol PL/mg chlorophyll; [j]µg PL/mg protein; [k]µg lipid P/g; [l]µmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]µmol PL/g dwb; [p]µg PL/100 mg fwb; [q]µg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]µmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]µg PL/mL; [x]µg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]µg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]µg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Capsicum frutescens* L. (Chili Pepper) | | | | | | | | | | | |
| 1 | Fruit | TLC | 12.6 | 26.6 | 12.7 | | | | 43.4 | 0.386 | 1446 |
| *Carica papaya* L. (Papaya) | | | | | | | | | | | |
| 1 | Seed | TLC | 28.1 | 18.7 | | 34.0 | | | (LPC +) | 0.15 | 1548 |
| *Carica pubescens* Lenné and K. Koch (Mountain Papaya) | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.67 | | | | | | 1566 |
| *Carthamus oxycantha* M. Rieb. (Wild Safflower) | | | | | | | | | | | |
| 1 | Seed | TLC | 36.7 | 29.4 | | 20.6 | | | | | 1567 |
| *Carthamus tinctorius* L. (Safflower) | | | | | | | | | | | |
| 1 | Seed, whole | TLC | 32 | 16 | | 23 | | | | 0.705 | 1568 |
| 1 | Seed | TLC | + | + | + | + | + | + | | (LPC +) | 1569 |
| 1 | Cotyledon, oil bodies | TLC | 57.6 | 15.0 | 0 | 25.4 | | 1.9 | | | 1570 |
| 1 | –, microsomes | TLC | 53.8 | 20.1 | 0 | 22.9 | | 3.1 | | | 1570 |
| 1 | Seed, oil body | TLC | | | | | 0 | | | | 1571 |
| *Carum carvi* L. (Caraway) | | | | | | | | | | | |
| 1 | Seed (wild form) | TLC | 46 | 20 | 2 | 20 | | 5 | 2 | 4.5[a] | 1438 |
| | | | also LPC trace, LPE 4. | | | | | | | | |
| 1 | Fruit | TLC | 41.5 | 18.6 | 7.5 | 18.6 | | 2.4 | | 0.5 | 1471 |
| | | | also LPC 3.1, LPE 4.3 | | | | | | | | |
| *Carum copticum* (L.) Benth. and Hook. (Bishop's Weed) | | | | | | | | | | | |
| 1 | Seed | TLC | 26 | 35 | | 26 | | (LPE 14) | | 0.84[c] | 1572 |
| *Carya illinoinensis* (Wangenh.) K. Koch (Pecan) | | | | | | | | | | | |
| 5 | Pollen | TLC | + | + | + | + | + | Trace | | | 1573 |
| *Caryocar coriaceum* Wittm. (Piqui) | | | | | | | | | | | |
| 1 | Seed | TLC | Trace | 28 | | 72 | | | | 0.20[c] | 1574 |
| *Cassia absus* L. (Pig's Senna) | | | | | | | | | | | |
| 1 | Seed[a] | TLC | 19.3 | 15.8 | | | | (LPC 0.7, LPE 1.3) | | 2.41 | 1575 |
| *Cassia fistula* L. (Golden Shower) | | | | | | | | | | | |
| 1 | Seed[a] | TLC | 22.6 | 18.2 | | | | (LPC 1.1, LPE 2.4) | | 2.35 | 1575 |
| 1 | Seed | CC (silica) | 35.6 | 64.4 | | | | | | | 1576 |
| *Cassia occidentalis* L. (Coffee Senna) | | | | | | | | | | | |
| 1 | Seed[a] | TLC | 23.3 | 17.2 | | | | (LPC 0.9, LPE 1.2) | | 1.90 | 1575 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Cassia tora* L. (Sicklepod) | | | | | | | | | | |
| 1 | Seed | TLC | 53.1 | 16.6 | 1.7 | 17.2 (incl. PS) | | 10.7 | 1.17 | 1577 |
| *Castanea crenata* Sieb. and Zucc. (Japanese Chestnut) | | | | | | | | | | |
| 3 | Seed, inner, free | TLC | 26.4-33.1 | 7.7-19.5 | 14.6-26.2 | 9.8-21.5 | | (LPC 11.5-25.5) | | 1578 |
| 3 | –, inner, bound | TLC | 32.0-40.4 | 6.3-10.4 | 9.9-20.8 | 26.7-32.3 | | (LPC 5.1-15.7) | | 1578 |
| 3 | –, outer, free | TLC | 18.6-30.7 | 9.0-22.9 | 14.3-24.1 | 21.4-34.8 | | (LPC 7.0-22.9) | | 1578 |
| 3 | Seed, outer, bound | TLC | 8.0-36.9 | 5.4-8.1 | 6.0-19.9 | 36.9-43.4 | | (LPC 5.9-24.0) | | 1578 |
| *Cattleya* spp. | | | | | | | | | | |
| 1 | Leaf | TLC | | | 10 | | | | | 1440 |
| *Cattleya bowringiana* Veitch. (Pine Ridge Orchid) | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.14 | | | | | 1402 |
| *Celosia argentea* L. (Cockscomb) | | | | | | | | | | |
| 1 | Seed | TLC | 43 | 35 | | 22 | | | 0.47 | 1458 |
| *Ceratodon purpureus* (Hedw.) Brid. | | | | | | | | | | |
| 1 | Protonemata | TLC | 55.8 | 11.6 | 20.4 | 12.2 | | | 2.12[m] | 1579 |
| *Ceratophyllum demersum* L. | | | | | | | | | | |
| 1 | Whole plant | TLC | 36.0 | 19.1 | 13.4 | 9.5 | 4.9 | 17.1 | 2.98[c] | 1445 |
| *Ceratophyllum submersum* L. | | | | | | | | | | |
| 1 | Whole plant | TLC | 44.0 | 16.5 | 14.8 | 16.4 | 4.9 | 2.6 | 6.28[c] | 1555 |
| *Ceratopteris thalictroides* (L.) Brongn. (Water Sprite) | | | | | | | | | | |
| 1 | Whole plant | TLC | 47.5 | 23.7 | 9.7 | 7.4 | 9.1 | Trace 4.4 | 3.00[c] | 1555 |
| *Chaerophyllum bulbosum* L. (Turnip-Rooted Chervil) | | | | | | | | | | |
| 1 | Seed | TLC | 49 also LPC 1. | 8 | 5 | 29 | | 6 1 | 1.2[a] | 1438 |
| *Chenopodium album* L. (Lambsquarters) | | | | | | | | | | |
| 1 | Leaf, thylakoid | TLC | 46 | | 42 | 12 | | | 983[q] | 1464 |
| 1 | Leaf, chloroplast | HPLC | 38.4 | 46.7 | 8.7 | 6.1 | | | 82.8[a] | 1465 |
| *Chenopodium quinoa* Willd. (Quinoa) | | | | | | | | | | |
| 1 | Seed | TLC | 13.2 also LPC 3.9, LPE 46.4 | 19.8 | | 11.3 | 4.3 | 1.2 | 1.77 | 1580 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]µmol PL/mg protein; [i]µmol PL/mg chlorophyll; [j]µg PL/mg protein; [k]µg lipid P/g; [l]µmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]µmol PL/g dwb; [p]µg PL/100 mg fwb; [q]µg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]µmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]µg PL/mL; [x]µg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]µg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]µg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, flour | TLC | 52.6 | 8.9 | | 13.7 | 2.9 | 0.4 | | 0.64 | 1580 |
| | | | also LPC 3.6, LPE 17.8 | | | | | | | | |
| 1 | –, bran | TLC | 49.1 | 13.6 | | 5.9 | 4.0 | 0.5 | | 1.45 | 1580 |
| | | | also LPC 4.3, LPE 22.7 | | | | | | | | |
| 1 | –, hull | TLC | 16.4 | 20.9 | | 10.1 | 3.3 | 0.6 | | 2.40 | 1580 |
| | | | also LPC 3.1, LPE 45.6 | | | | | | | | |
| *Chenopodium rubrum* L. (Red Goosefoot) | | | | | | | | | | | |
| 1 | Cell culture | TLC | 76 | 24 | Trace | | | | | 1.65[c] | 1581 |
| *Cicer arietinum* L. (Chickpea) | | | | | | | | | | | |
| 1 | Seed, immature[g] | TLC | 8.1 | 12.6 | | 18.4 | | 3.2 | 4.8 | | 1582 |
| 1 | Seed, mature[g] | TLC | 39.3 | 30.6 | | 0.9 | | 1.4 | 4.1 | | 1582 |
| 1 | –, dehulled[g] | TLC | 37.4 | 33.4 | | 1.7 | | 1.1 | 4.7 | | 1582 |
| 1 | Root, 6 days old | TLC | 34.3 | 27.3 | 6.5 | 6.2 | 8.2 | 6.1 | 5.7 | 0.83 | 1583 |
| *Cicer soongaricum* DC (Channa) | | | | | | | | | | | |
| 1 | Seed | TLC | 50.0 | 38.0 | | Trace | 11.9 | | | 2.15 | 1584 |
| *Cichorium intybus* L. (Chicory) | | | | | | | | | | | |
| 1 | Root[l] | Choline | 2 | | | | | | | | 1451 |
| *Cistus ladanifer* L. (Rockrose) | | | | | | | | | | | |
| 1 | Seed | TLC | 46 | 32 | 10 | 12 | | | | 0.54[c] | 1585 |
| | | No significant variation in seeds of 15 other *Cistus* spp. | | | | | | | | | |
| *Citrofortunella mitis* Blanco (Calamondin) | | | | | | | | | | | |
| 1 | Fruit outer peel, leucoplast[g] | TLC | 43.0 | 4.6 | 2.5 | 6.6 | | | Trace | | 1586 |
| *Citrullus colocynthis* (L.) Schrad. (Colocynth) | | | | | | | | | | | |
| 1 | Seed | TLC | 41 | 17 | 14 | 11 | | | 16 | 5.66[c] | 1524 |
| *Citrullus vulgaris* Schrad. (Watermelon) | | | | | | | | | | | |
| 1 | Seed | TLC | 36.1 | 8.6 (incl. PG) | | 30.4 | | (LPC 6.6, LPE 6.4) | | | 1587 |
| 3 | Seed | TLC | 24.7-26.1 | 23.8-27.1* | | 14.3-19.7 | 6.7-8.6 | (LPC 12.8-19.0) | | 0.30-0.59 | 1588 |
| | | *Incl. MGDG | | | | | | | | | |
| 1 | Cotyledon[a] | TLC | 2.8 | 2.4 | | 2.8 | | (LPC 2.4) | | | 1589 |
| 1 | Root[a] | TLC | 3.5 | 3.1 | | 2.9 | | (LPC 2.0) | | | 1589 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Citrullus vulgaris* ssp. *fistulosus* (Squash Melon) | | | | | | | | | | | |
| 1 | Seed | TLC | 34.1 | 10.9 (incl. PG) | | 25.4 | | (LPC 4.7, LPE 6.4) | | | 1587 |
| *Citrus aurantifolia* (Christm.) Swingle (Key Lime) | | | | | | | | | | | |
| 1 | Leaf | TLC | 73.7 | 15.8 | 6.7 | 3.8 | | | | 0.495 | 1590 |
| *Citrus aurantium* L. (Sour Orange) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | + | + | | | | | 1591 |
| *Citrus iyo* hort. ex Tanaka (Iyomikan) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | + | + | | | 0.25 | 1592 |
| *Citrus jambhiri* Lush. (Rough Lemon) | | | | | | | | | | | |
| 1 | Leaf | TLC | 68.3 | 19.5 | 8.3 | 3.9 | | | | 0.508 | 1590 |
| *Citrus junos* (Sieb.) Tanaka (Yuzu) | | | | | | | | | | | |
| 1 | Seed, kernel | TLC | 55.3 | 24.9 | | 3.5 | 9.4 | 1.6 | (LPC 4.0) | | 1593 |
| 1 | –, coat | TLC | 47.8 | 31.4 | | 4.5 | 5.1 | 1.4 | (LPC 7.6) | | 1593 |
| 1 | Leaf | TLC | 21.0 | 13.7 | 29.8 | 35.5 | | | | 0.58 | 1594 |
| 1 | Leaf | TLC | + | + | | + | + | | | | 1595 |
| *Citrus limon* (L.) Burm.f. (Lemon) | | | | | | | | | | | |
| 1 | Juice | TLC | 41 | 38 | | 15 | 5 | 2 | | 1.15[b] | 1596 |
| 1 | Leaf | TLC | + | + | | + | + | | | | 1595 |
| 1 | Leaf | TLC | 47.8 | 35.8 | 8.6 | 7.8 | | | | 0.232 | 1590 |
| *Citrus medica* L. (Citron) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | + | + | | | | | 1591 |
| *Citrus medioglobosa* hort. ex Tanaka (Naruto) | | | | | | | | | | | |
| 1 | Fruit, flavedo | TLC | 52 | 36 | | 12 | | | | 1.16[l] | 1597 |
| *Citrus natsudaidai* Hayata (Natsudaidai) | | | | | | | | | | | |
| 2 | Seed | TLC | + | + | | + | + | | | 0.21-0.53 | 1592 |
| 1 | Leaf | TLC | 54.0 | 20.6 | 27.7 | | | | | 0.97 | 1598 |
| *Citrus* × *paradisi* Macf. (Grapefruit) | | | | | | | | | | | |
| 1 | Leaf | TLC | 57.2 | 27.7 | 8.7 | 6.3 | | | | 0.332 | 1590 |
| 1 | Fruit, juice | TLC | 47 | 36 | | 12 | 1 | 1 | | 0.67[b] | 1596 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]µmol PL/mg protein; [i]µmol PL/mg chlorophyll; [j]µg PL/mg protein; [k]µg lipid P/g; [l]µmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]µmol PL/g dwb; [p]µg PL/100 mg fwb; [q]µg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]µmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]µg PL/mL; [x]µg lipid P/cm$^2$ leaf area; [y]Molecules per 10$^6$ plastids; [z]µg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]µg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *C. paradisi* Macf. × *C. reticulata* Blanco (Tangelo) | | | | | | | | | | | |
| 1 | Leaf | TLC | 62.1 | 19.0 | 5.9 | 13.1 | | | | 0.153 | 1590 |
| *Citrus reticulata* Blanco (Tangerine) | | | | | | | | | | | |
| 3 | Leaf | TLC | 55.2-65.2 | 15.1-17.0 | 6.7-10.3 | 9.7-13.7 | | | | 0.135-0.165 | 1590 |
| *Citrus sinensis* (L.) Osbeck (Orange) | | | | | | | | | | | |
| 1 | Seed | TLC | 25.2 | 28.3 | | 30.2 | | | 16.3 | | 1550 |
| 1 | Leaf | TLC | + | + | | + | + | | | | 1595 |
| 1 | Fruit juice | TLC | 41 | 38 | | 8 | 3 | 7 | | 1.31[b] | 1596 |
| 1 | –, chromoplast | TLC | 48 | 42 | 0 | | | | | 1.41[l] | 1599 |
| 1 | Fruit flavedo, chloroplast | TLC | Trace | Trace | <90 | | | | | 0.39[l] | 1599 |
| 1 | –, chromoplast | TLC | Trace | Trace | >90 | | | | | 0.52[l] | 1599 |
| 1 | Fruit, essential oil | TLC | + | 0 | | | | | 0 | | 1600 |
| (*C. sinensis* × *C. reticulata*) × *C. reticulata* Blanco (Mandarin) | | | | | | | | | | | |
| 1 | Leaf | TLC | 50.8 | 33.1 | 4.0 | 12.1 | | | | 0.124 | 1590 |
| *Citrus sudachi* hort. ex Shirai (Sudachi) | | | | | | | | | | | |
| 1 | Seed, kernel | TLC | 57.0 | 23.9 | | 4.0 | 9.3 | 1.9 | (LPC 3.4) | | 1593 |
| 1 | –, coat | TLC | 45.1 | 32.3 | | 5.9 | 7.9 | 1.1 | (LPC 6.0) | | 1593 |
| *Citrus tamurana* hort. ex Tanaka (Hyuganatsu) | | | | | | | | | | | |
| 1 | Fruit juice | TLC | + also LPC +, LPE + | + | | + | + | + | | 3.3[b] | 1601 |
| *Citrus unshiu* Marc. (Mandarin) | | | | | | | | | | | |
| 1 | Fruit, flavedo | TLC | 33.9 also LPC 0.3, LPE 0.2 | 37.5 | 10.6 | 4.7 | 1.5 | 6.9 | 4.4 | 0.34 | 1602 |
| 1 | –, albedo | TLC | 16.2 also LPC 0, LPE 0 | 37.0 | 15.1 | 14.5 | 6.7 | 3.6 | 6.9 | 0.10 | 1602 |
| 1 | –, membrane | TLC | 26.1 also LPC 0.9, LPE 0.5 | 28.5 | 19.7 | 11.8 | 5.4 | 1.4 | 5.7 | 0.23 | 1602 |
| 1 | –, flesh | TLC | 34.9 also LPC 2.3, LPE 1.2 | 32.4 | 12.4 | 7.5 | 2.5 | 4.9 | 1.9 | 0.04 | 1602 |
| *Citrus yuko* hort. ex Tanaka (Yuko) | | | | | | | | | | | |
| 1 | Seed, kernel | TLC | 50.4 | 28.6 | | 2.3 | 11.2 | 1.7 | (LPC 4.4) | | 1593 |
| 1 | –, coat | TLC | 42.7 | 37.7 | | 3.1 | 6.2 | 1.0 | (LPC 7.4) | | 1593 |
| *Clarkia rubicunda* (Lindl.) Lewis | | | | | | | | | | | |
| 1 | Pollen | TLC | + | + | | + | | | | | 1603 |
| | Of 69 spp. of angiosperm pollens collected in California, 77% contained PC, 54% PE, 6% PG, and 48% PI. | | | | | | | | | | |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Climacium dendroides* (Hedw.) Web. et Mokr. | | | | | | | | | | | |
| 1 | Whole plant | TLC | 67.0 | 11.4 | 10.0 | 4.0 | 4.2 | | | 0.60[c] | 1493 |
| *Cochlearia anglica* L. (English Scurvy Grass) | | | | | | | | | | | |
| 1 | Root | TLC | 39.0 | 39.1 | 4.5 | 6.2 | | 12.1 | | 0.83[e] | 1604 |
| *Cocos nucifera* L. (Coconut) | | | | | | | | | | | |
| 1 | Nut, kernel | TLC | 34.6 | 24.6 | | 19.0 | 4.8 | 2.5 | | 0.20[a] | 1605 |
| | | | also LPC 4.6 and LPE 3.4 | | | | | | | | |
| *Coffea arabica* L. (Coffee) | | | | | | | | | | | |
| 3 | Bean[s] | | + | | | | | | | | 1606 |
| 1 | Leaf | TLC | 52 | 15 | 22 | 11 | | | | | 1607 |
| *Coix lacryma-jobi* L. (Adlay, Job's Tears) | | | | | | | | | | | |
| 1 | Seed, brown | TLC | 43.0 | 27.5 | | 13.0 | 2.4 | (LPC 3.3) | | 1.83 | 1608 |
| 1 | –, polished | TLC | 48.4 | 24.9 | | 7.4 | 4.0 | (LPC 3.9) | | 1.78 | 1608 |
| *Colocasia esculenta* (L.) Schott (Taro) | | | | | | | | | | | |
| 1 | Leaf | TLC | 46.9 | 10.7 | 19.9 | 16.2 | 6.6 | | | 2.63[c] | 1470 |
| 1 | Stalk | TLC | 38.3 | 18.4 | 24.7 | 13.6 | 5.1 | | | 1.11[c] | 1470 |
| 1 | Cormel, peeled | TLC | + | + | | | | | (LPC +) | | 1609 |
| *Concephalum conicum* (L.) Corda (Scented Liverwort.) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Convallaria majalis* L. (Lily of the Valley) | | | | | | | | | | | |
| 1 | Leaf | TLC | | | 14 | | | | | | 1440 |
| *Conyza canadensis* L. (Horseweed) | | | | | | | | | | | |
| 1 | Leaf, chloroplast[a] | TLC | 8.6 | 5.5 | 7.0 | | | | | 2.68[i] | 1610 |
| *Coriandrum sativum* L. (Coriander) | | | | | | | | | | | |
| 1 | Seed | TLC | 44.0 | 29.3 | | 23.1 | | | | 0.1 | 1548 |
| 1 | –, coat endosperm | TLC | 49 | 21 | | 12 | | 19 | | | 1611 |
| 1 | Fruit | TLC | 46.1 | 18.4 | | 22.4 | | 6.6 | | 0.3 | 1471 |
| | | | also LPC 3.5, LPE 1.8 | | | | | | | | |
| *Corylus avellana* L. (European Hazel) | | | | | | | | | | | |
| 1 | Seed, cotyledon | TLC | 37.8 | 47.2 | 5.5 | 8.9 | | 0.6 | | | 1612 |
| 1 | –, embryonic axis | TLC | 54.6 | 32.3 | 8.0 | 5.1 | | | | | 1612 |
| 1 | Seed, kernel[a] | HPLC | 0.075 | 0.019 | | 0.015 | | | | | 1613 |
| | and weekly changes during development 134-176 daf | | | | | | | | | | |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Seedling, plumule | TLC | 33.4 | 45.6 | 3.0 | 18.0 | | | | | 1612 |
| 1 | –, root, and hypocotyl | TLC | 29.8 | 39.8 | 10.5 | 19.9 | | | | | 1612 |
| 1 | –, petiole | TLC | 36.2 | 39.6 | 8.2 | 16.0 | | | | | 1612 |
| 1 | –, cotyledon | TLC | 38.0 | 27.0 | 19.4 | 10.2 | | 5.4 | | | 1612 |
| *Crambe abyssinica* Hochst (Crambe) | | | | | | | | | | | |
| 1 | Seed | TLC | 34.6 | 24.4 | | 27.0 | 6.4 | | | | 1614 |
| *Crambe amabilis* Butkov and Majlin | | | | | | | | | | | |
| 1 | Seed | TLC | 56.1 | 20.6 | | 13.2 | 3.0 | | | 0.85[c] | 1615 |
| | | | also NAPE 2.8, NALPE 2.3, LPC 2.0 | | | | | | | | |
| 1 | Leaf | TLC | 23.0 | 25.2 | 3.0 | 33.4 | | 8.3 | | 0.15[c] | 1616 |
| | | | also NAPE 3.5, NALPE 2.6, LPC 1.0 | | | | | | | | |
| 1 | Flower | TLC | 37.2 | 21.0 | 2.0 | 20.2 | 5.4 | 2.2 | | 0.63[c] | 1616 |
| | | | also NAPE 4.5, NALPE 3.2, LPC 4.3 | | | | | | | | |
| 1 | Stem | TLC | 24.0 | 23.0 | 5.5 | 25.2 | 5.4 | 6.5 | | 0.10[c] | 1616 |
| | | | also NAPE 4.4, NALPE 4.0, LPC 2.0 | | | | | | | | |
| *Crambe schugnana* Korch. | | | | | | | | | | | |
| 1 | Seed | TLC | 55.0 | 13.7 | | 19.0 | 4.6 | | | 0.69[c] | 1617 |
| | | | also NAPE 3.4, LPC 4.3 | | | | | | | | |
| *Crataegus turkestanica* Pojark. (Turkestan Hawthorn) | | | | | | | | | | | |
| 1 | Fruit, kernel | TLC | 61.5 | 8.7 | | 27.9 | | 1.7 | | 0.03 | 1618 |
| 1 | Pericarp | TLC | 60.1 | 23.8 | Trace | 10.3 | | 1.7 | | 0.21 | 1619 |
| *Crotalaria juncea* L. (Sunn Hemp) | | | | | | | | | | | |
| 1 | Pollen | TLC | 8.2 | 23.8 | 12.9 | 9.9 | 13.9 | 31.3 | | | 1620 |
| *Crotalaria retusa* L. (Rattleweed) | | | | | | | | | | | |
| 1 | Pollen grain | TLC | 58.6 | 27.3 | 8.6 | 8.8 (incl. PS) | | | | 5.49[c] | 1621 |
| *Ctenidium molluscum* (Hedw.) Mitt. (Mollusc Ctenidium Moss) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Cucumis melo* L. (Sweet Melon) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | | | | | 4-10 | 1622 |
| *Cucumis melo* L. ssp. *reticulatus* (Muskmelon) | | | | | | | | | | | |
| 1 | Seed, kernel | TLC | 26.0 | 29.3 | 7.9 | 10.2 | 5.0 | 3.1 | | 1.04[c] | 1623 |
| | | | also LPC 8.8, LPE 9.7 | | | | | | | | |
| *Cucumis sativus* L. (Cucumber) | | | | | | | | | | | |
| 1 | Cotyledon | TLC | 39 | 29 | | 29 | | 3 | | 1.80[l] | 1447 |
| 1 | Cotyledon, 7 days[a] | TLC | 21 | 4 | 2 | | | | | | 1403 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, protoplast[a] | TLC | 8 | 5 | 8 | | | | | | 1403 |
| 1 | Leaf | TLC | 34.9 | 21.5 | 22.6 | 7.2 | 4.6 | 4.6 | 4.6 | 1.95[l] | 1624 |
| 1 | Leaf, thylakoid[s] | | + | | + | | | | | | 1625 |
| 1 | –, LH (II)[s] | | + | | 35.5 | | | | | | 1625 |
| 1 | Fruit, whole | TLC | 45.6 | 31.3 | 6.4 | 5.0 | 2.2 | 0.7 | | 0.050 | 1563 |
| | | | also LPC 3.2 and LPE 1.0 | | | | | | | | |
| 1 | Fruit, peeled and deseeded | TLC | 50.8 | 36.5 | 4.4 | 4.4 | 0.4 | 0.9 | 1.8 | 45.5[a] | 1626 |
| | | | also LPC 0.4 and LPE 0.8 | | | | | | | | |
| 2 | Root | TLC | 25.5-29.6 | 38.4-40.5 | 0.9-2.0 | 14.8-19.0 | 7.2-12.0 | 25.8-44.6 | | 15.3-21.6[k] | 1627 |
| *Cucurbita digitata* Gray (Coyote Gourd) | | | | | | | | | | | |
| 1 | Seed | TLC | 74.9 | 10.5 | | 13.7 | | | (LPC trace) | 3.3[a] | 1476 |
| *Cucurbita ficifolia* Bouchè (Figleaf Gourd) | | | | | | | | | | | |
| 1 | Leaf | TLC | | | 3.60[a] | | | | | 3.26[l] | 1628 |
| 1 | Root | TLC | 32.4 | 30.0 | 8.4 | 15.0 | 11.3 | 21.5 | | 21.3[k] | 1627 |
| *Cucurbita foetidissima* HBK (Calabazilla) | | | | | | | | | | | |
| 1 | Seed | TLC | 55.8 | 18.7 | | 17.2 | | | (LPC 0.8) | 2.9[a] | 1476 |
| *Cucurbita maxima* Duch. (Hubbard Squash) | | | | | | | | | | | |
| 3 | Seed | TLC | 22.1-24.6 | 15.4-23.6 | | 18.6-23.2 | 18.0-18.9 | | | 1.23-1.57 | 1629 |
| 1 | Leaf[i] | TLC | 3.75 | 3.75 | 3.74 | | | | | | 1630 |
| *Cucurbita moschata* Duch. (Warty Squash) | | | | | | | | | | | |
| 1 | Seed | TLC | 21.6 | 22.0 | | 16.0 | 16.4 | | | 2.12 | 1629 |
| 1 | Leaf | TLC | + | + | + | + | | | | | 1631 |
| 1 | Leaf thylakoid membrane[a] | TLC | | | 10.9 | | | | | | 1632 |
| *C. maxima* × *C. moschata* | | | | | | | | | | | |
| 1 | Seed | TLC | 25.4 | 25.9 | | 18.4 | 18.8 | | | 1.64 | 1629 |
| *Cucurbita pepo* L. (Pumpkin) | | | | | | | | | | | |
| 1 | Leaf | TLC | 43 | 27 | 24 | 4 | | | 2 | 3.74[l] | 1523 |
| 1 | –, mitochondria | TLC | 15.9 | 35.0 | 15.1 | 4.0 | 7.4 | 11.9 | 7.5 | 0.050[c] | 1633 |
| 1 | Leaf | TLC | 36.7 | 26.6 | 21.6 | 12.2 | 2.9 | | | 1651[r] | 1634 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Root meristem | TLC | 31.5 | 50.1 | | 6.3 | 3.5 | 6.6 | 2.7 | | 1635 |
| *Cucurbita pepo* L. ssp. *melopepo* (Zucchini Squash) | | | | | | | | | | | |
| 1 | Fruit, epidermis | TLC | 48.8 | 33.7 | 14.9 | 2.6 | | | | 0.39[c] | 1636 |
| *Cuminum cyminum* L. (Cumin) | | | | | | | | | | | |
| 1 | Seed | TLC | 35.0 | 49.0 | 4.0 | 7.0 | | | (LPE 5.0) | 0.74[c] | 1637 |
| 1 | Fruit | TLC | 47.6 | 11.6 | | 20.1 | | 6.7 | | 0.5 | 1471 |
| | | | also LPC 4.1, LPE 3.9 | | | | | | | | |
| *Cupressus dupreziana* A. Camus (Saharan Cypress) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | | | | | | | 1436 |
| *Cuscuta reflexa* Roxb. (Dodder) | | | | | | | | | | | |
| 1 | Whole vine | TLC | 39.3 | 26.6 | 11.9 | 19.7 | | 2.5 | | 0.208 | 1638 |
| *Cycas tharwanara* | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | | | | | | | 1436 |
| *Cyclamen persicum* Mill. (Cyclamen) | | | | | | | | | | | |
| 1 | Leaf | TLC | | | | | + | | | | 1450 |
| *Cydonia oblonga* Mill. (Quince) | | | | | | | | | | | |
| 1 | Seed | TLC | 30.5 | 6.0 | 4.1 | 28.7 | | 6.7 | 4.4 | 0.3 | 1639 |
| | | | also LPC 3.5, LPE 5.4 | | | | | | | | |
| *Cymbidium* hybrid Sw. | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.21 | | | | | | 1402 |
| 1 | Leaf | TLC | | | 12 | | | | | | 1440 |
| *Cynoglossum officinale* L. (Hound's Tongue) | | | | | | | | | | | |
| 1 | Seed (NAPE +) | TLC | + | + | | + | | + | | 0.4 | 1640 |
| *Cyperus esculentus* L. (Yellow Nutsedge, Chufa) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | + | + | | + | (LPC +) | | 1569 |
| 1 | Tuber | TLC | 35.0 | 22.0 | | 16.0 | 1.7 | | | 5.60[a] | 1641 |
| *Cypripedium insigne* Wall. (Large-Flowered Lady's Slipper) | | | | | | | | | | | |
| 1 | Leaf | TLC | | | 8 | | | | | | 1440 |
| *Dactylis glomerata* L. (Orchard Grass, Cocksfoot) | | | | | | | | | | | |
| 1 | Leaf | TLC | 33 | 24 | 33 | 3 | | | 8 | 3.38[l] | 1523 |
| 1 | Seedling, plasma membrane | TLC | 43.5 | 37.3 | 10.6 | 7.2 (incl. PS) | | 1.3 | 0 | 1.05[t] | 1642 |
| 1 | –, endopl. reticulum and golgi membrane | TLC | 45.7 | 27.1 | 14.4 | 10.5 (incl. PS) | | 0.8 | 1.4 | 1.11[t] | 1642 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, mitochondria | TLC | 39.8 | 34.7 | 9.9 | 4.5 (incl. PS) | | 2.2 | 8.7 | 0.44[t] | 1642 |
| *Datura inoxia* Mill. (Downy Thorn Apple) | | | | | | | | | | | |
| 1 | Leaf[a] | TLC | | | | 4 | | | | | 1643 |
| 1 | Callus cell culture | TLC | 33 | 19 | 6 | 28 | 9 | 5 | | 1.68[c] | 1643 |
| *Daucus carota* L. (Carrot) | | | | | | | | | | | |
| 1 | Seed | TLC | 29.1 | 35.4 | | 23.1 | | | 8.6 | 0.12 | 1548 |
| 1 | Seed | TLC | | | | | | $P_{NAPE}/P_{total}$ 1.1 | | | 1497 |
| 1 | Leaf | TLC | 30.9 | 25.2 | 29.5 | 14.4 | Trace | | | 1128[r] | 1634 |
| 1 | Fruit | TLC | 48.2 | 11.9 | 0.9 | 30.1 | | 3.2 | | 0.4 | 1471 |
| | | | also LPC 3.1, LPE 0.2 | | | | | | | | |
| 1 | Root[k] | PC | 2.36 | 2.47 | | 2.28 | | 3.40 | 1.12 | | 1644 |
| 1 | Root | TLC | 39 | 26 | 11 | 8 | 6 | 4 | | 0.055 | 1645 |
| 3 | Root[l] | Choline | 47.83 | | | | | | | | 1451 |
| 1 | Root | HPLC | 54 | 27 | | 9 | | 9 | | 0.79 | 1646 |
| 1 | Cell culture[a] | TLC | 30.4 | 16.8 | 0.9 | 9.1 | Trace | 0.6 | 1.3 | | 1647 |
| 1 | Cell suspension culture | TLC | 44.7 | 39.1 | 3.8 | | 12.4 | | | | 1648 |
| 1 | –, microsomal membrane | TLC | 50.8 | 29.8 | 5.9 | 7.5 | | 6.0 | | 0.43[l] | 1649 |
| *Daucus carota* L. ssp. *carota* (Wild Carrot) | | | | | | | | | | | |
| 1 | Pericarp, endosperm | TLC | 39 | 20 | | 12 | | 29 | | | 1611 |
| *Delonix regia* ([Boj.ex] Hook.) Raf. (Royal Poinciana, Flamboyant) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | | | (LPC +) | | | 1428 |
| *Dendrobium kingianum* Bidw. | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.40 | | | | | | 1402 |
| *Deschampsia antarctica* Desv. | | | | | | | | | | | |
| 1 | Leaf | TLC | 24 | 34 | 8 | 34 | | | | 1.07[l] | 1650 |
| 1 | Root | TLC | 23 | 25 | 22 | 30 | | | | 1.58[l] | 1650 |
| *Dianthus caryophyllus* L. (Carnation) | | | | | | | | | | | |
| 1 | Flower, petal | TLC | 23 | 10 | 45.2 | 17 | | 4.9 | | | 1651 |
| 1 | –, microsomal membrane | TLC | 40 | 28 | 18 | 5 | | | | | 1652 |
| *Diapensia lapponica* L. | | | | | | | | | | | |
| 1 | Leafy top[n] | TLC | 1.4 | 1.0 | 0.4 | | | 0.2 | | 0.33[c] | 1653 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Dicranella heteromolla* (Hedw.) Schimp. (Dicranella Moss) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Dicranum polysetum* Sw. (Dicranum Moss) | | | | | | | | | | | |
| 1 | Whole plant *Incl. LPE | TLC | 58.9 | 17.7 | 8.8 | 11.7* | 2.9 | | | 0.68[c] | 1654 |
| *Digitaria sanguinalis* (L.) Scop. (Hairy Crabgrass) | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 1.08 | | | | | | 1402 |
| *Dioscorea aimadoimo* (Korean Yam) | | | | | | | | | | | |
| 1 | Tuber | TLC | 45.2 | 38.1 | | 13.9 | | | | 0.230 | 1655 |
| *Dioscorea alata* L. (Winged Yam) | | | | | | | | | | | |
| 1 | Tuber | TLC | 8 | 19 | 15 | 16 | 32 | | | 0.22[c] | 1656 |
| *Dioscorea batatas* Decne. (Chinese Yam) | | | | | | | | | | | |
| 1 | Tuber | TLC | 26.4 | 29.3 | | 32.9 | | | | 0.107 | 1655 |
| *Dioscorea bulbifera* L. (Air Potato) | | | | | | | | | | | |
| 1 | Tuber | TLC | 42 | 20 | 12 | 13 | 6 | | | 0.23[c] | 1656 |
| *Dioscorea cayenensis* Lam. (Yellow Guinea Yam) | | | | | | | | | | | |
| 1 | Tuber | TLC | 42 | 21 | 11 | 13 | 6 | | | 0.10[c] | 1656 |
| *Dioscorea japonica* Thunb. (Japanese Yam) | | | | | | | | | | | |
| 1 | Tuber | TLC | 43.4 | 37.2 | | 15.8 | | | | 0.081 | 1655 |
| *Dioscorea opposita* Thunb. (Chinese Yam) | | | | | | | | | | | |
| 1 | Rhizome | TLC | 39.5 | 12.7 | | 1.8 | | (LPC 8.2) | | 0.161 | 1657 |
| *Dioscorea rotundata* Poir. (White Guinea Yam) | | | | | | | | | | | |
| 1 | Tuber | TLC | 42 | 20 | 12 | 13 | 6 | | | 0.03[c] | 1656 |
| *Diospyros kaki* L.f. (Japanese Persimmon, Kaki) | | | | | | | | | | | |
| 3 | Seed[g] | TLC (MeNH-PE 2.5-4.2, $Me_2N$-PE 3.8-4.7) | | | | 8.3-10.3 | | | | 0.11-0.18[d] | 1658 |
| 1 | Fruit, flesh | TLC | 20.0 | 8.8 | 29.8 | 13.5 | 7.0 | 4.2 | 16.7 | 0.026 | 1659 |
| 1 | Fruit, rind | TLC | 26.3 | 7.0 | 46.5 | 13.2 | 1.8 | 0 | 0 | 0.049 | 1659 |
| 1 | Fruit, flesh | TLC | 28.2 | 5.0 | 37.0 | 11.0 | 13.0 | 1.9 | 3.9 | 0.037 | 1659 |
| 1 | –, rind | TLC | 18.8 | 6.2 | 37.5 | 12.5 | 25.0 | 1.8 | 3.5 | 0.012 | 1659 |
| *Diptychocarpus strictus* (Fisch.) Trautv. | | | | | | | | | | | |
| 1 | Seed | TLC | 50.2 | 12.2 | | 22.9 | | (LPC 10.4) | | 0.45[c] | 959 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Seed | TLC | | | | | | (NAPE 1.9) | | | 1660 |
| *Drepanocladus lycopodioides* (Brid.) Warnst. | | | | | | | | | | | |
| 1 | Whole plant | TLC | 32.2 | 21.3 | 32.4 | 4.9 | 6.6 | | | 1.19[c] | 1551 |
| *Dryopteris dilatata* (Hoffm.) A. Gray | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Dryopteris filix-mas* (L.) Schott. (Shield Fern) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | + | + | | | | 0.91 | 1661 |
| *Echinochloa colona* (L.) Link (Barnyard Millet) | | | | | | | | | | | |
| 1 | Grain | TLC | 30.7 | 24.0 | 3.8 | 6.6 | 8.3 | 1.8 | (LPC 24.8) | 0.44[c] | 1662 |
| *Eichhornia crassipes* (Mart.) Solms (Water Hyacinth) | | | | | | | | | | | |
| 1 | Leaf | TLC | 11.4 | 25.4 | 30.7 | 18.9 | 3.8 | | 9.8 | 3.93[c] | 1663 |
| 1 | Leaf stalk | TLC | 26.7 | 21.7 | 30.0 | 21.7 | 0 | | 0 | 0.05[c] | 1663 |
| 1 | Flower | TLC | 31.3 | 34.2 | 23.5 | 0 | 0 | | 11.0 | 1.77[c] | 1663 |
| 1 | Root | TLC | 40.2 | 27.7 | 26.0 | 0 | 0 | | 6.1 | 0.37[c] | 1663 |
| 1 | Whole plant | HPLC | The PC contains a pentacos-17-enoic acid group and the PE, a nonadec-6-enoic acid group | | | | | | | | 1664 |
| *Elaeagnus angustifolia* L. (Russian Olive) | | | | | | | | | | | |
| 1 | Seed | TLC | 52.1 | 16.4 | | 19.2 | | 3.5 | | (NAPE 1.7, NALPE 3.2) | 1665 |
| 1 | Fruit, pericarp | TLC | 45.8 | 25.0 | | 29.2 | | | | | 1665 |
| *Elaeis guineensis* Jacq. (Oil Palm) | | | | | | | | | | | |
| 1 | Kernel, haustorium | TLC | + | | | + | | | | | 1666 |
| 2 | Pollen | TLC | + | + | | + | | | | | 1667 |
| 1 | Fruit, mesocarp | TLC | 36 | 24 | 9 | 22 | Trace | 3 | 4 | 0.1-0.2 | 1668 |
| | | | also LPC trace and LPE 2. | | | | | | | | |
| *Elettaria cardamomum* (L.) Maton. (Cardamom) | | | | | | | | | | | |
| 1 | Seed | TLC | | 22.7 | | 4.9 | 6.5 | | 55.7 | 0.065 | 1669 |
| | | | also LPC 1.4, $Me_2$N-PE 8.8 | | | | | | | | |
| 1 | Pod ($Me_2$N-PE 49.5) | TLC | | | | 50.5 | | | | 4.4[a] | 1669 |
| *Eleusine indica* (L.) Gaertn. (Goosegrass) | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.70 | | | | | | 1402 |
| *Elodea canadensis* Michx. (Canadian Waterweed) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 47.6 | 18.8 | 11.3 | 11.4 | 8.4 | 2.5 | | 2.71[c] | 1445 |
| 1 | Leaf chloroplast | TLC | + | + | + | | | | | | 1670 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/$cm^2$ leaf area; [s]nmol PL/$cm^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/$cm^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Elodea nuttallii* (Planch.) H. St. John (Western Waterweed) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 46.6 | 19.0 | 20.2 | 11.7 | 2.5 | | Trace | 7.33[c] | 1555 |
| *Elyna spicata* Schrad. | | | | | | | | | | | |
| 1 | Leaf | TLC | 47 | 20 | 22 | 8 | | | 3 | 0.26 | 1441 |
| *Encyclia fragrans* Swartz. | | | | | | | | | | | |
| 1 | Leaf | TLC | | | 11 | | | | | | 1440 |
| *Ephedra gerardiana* Wall. ex Stapf. (Gerard Joint Fir) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | | | | | | | 1436 |
| *Epidendron radicans* Pav. ex Lindl. (Fiery Reed Orchid) | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.22 | | | | | | 1402 |
| *Equisetum arvense* L. (Field Horsetail) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Equisetum scirpoides* Michx. (Dwarf Scouring Bush) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Equisetum sylvaticum* L. (Woodland Horsetail) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Eriobotrya japonica* (Thunb.) Lindley (Loquat) | | | | | | | | | | | |
| 2 | Seed[a] | TLC | | 12.8-18.9 PS, 5.8-12.2 $Me_2N$-PE | | | | | | | 1671 |
| *Eruca sativa* Mill. (Rocket Salad, Taramira) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | + | | + | (LPC +, LPE +) | | 1672 |
| *Erysimum diffusum* Ehrh. (Gray Wallflower) | | | | | | | | | | | |
| 1 | Seed | TLC | 49.1 | 19.3 | | 21.3 | | | | 0.5[c] | 1673 |
| | | | also NAPE 3.2, NALPE 2.1, LPC 5.0 | | | | | | | | |
| *Erysimum sylvestris* (L.) Bess. | | | | | | | | | | | |
| 1 | Seed | TLC | 45.2 | 19.2 | | 16.4 | | | | 1.0[c] | 1673 |
| | | | also NAPE 7.0, NALPE 5.2, LPC 7.0 | | | | | | | | |
| *Euonymus europaeus* L. (European Spindle Tree) | | | | | | | | | | | |
| 1 | Seed, embryo | TLC | 49 | 25 | | 23 | | | | 262[w] | 1674 |
| *Euonymus japonica* Thunb. (Japanese Spindle Tree) | | | | | | | | | | | |
| 1 | Leaf | TLC | 54 | 15 | 18 | 12 | | | | | 1607 |
| *Fagopyrum esculentum* Moench (Buckwheat) | | | | | | | | | | | |
| 1 | Flour | TLC | 38.5 | 21.4 | | 2.2 | 14.8 | 7.0 | | 3.4 | 1675 |
| | | | also LPC 6.2, LPE 4.5, LPS 5.3 | | | | | | | | |
| 1 | Flour starch | TLC | 23.5 | 28.3 | 7.8 | 4.5 | | | | 0.045 | 1676 |
| | | | also LPC 24.8, LPE 4.0 | | | | | | | | |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Fagus sylvatica* L. (European Beech) | | | | | | | | | | | |
| 1 | Seed | TLC | Trace | 44.9 | | 55.1 | | | | 0.28[c] | 1677 |
| 1 | Leaf | TLC | 40.0 | 23.4 | 27.5 | 8.8 | Trace | | | 80[r] | 1634 |
| *Feijoa sellowiana* O. Berg. (Feijoa) | | | | | | | | | | | |
| 1 | Fruit, flesh | TLC | 16.4 | 7.2 | 19.3 | 10.8 | | 36.7 | 8.1 | 0.08 | 1678 |
| 1 | –, peel | TLC | 12.6 | 10.1 | 42.0 | 19.3 | | 8.4 | 7.6 | 0.18 | 1678 |
| *Ferula jaeschkeana* Vatke | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 1.5 | 794 |
| *Ferula karataviensis* (Rgl. and Schmalh.) Korov. | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 0.8 | 794 |
| *Ferula kelleri* K.-Pol. | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 0.5 | 794 |
| *Ferulago silvatica* Bess. | | | | | | | | | | | |
| 1 | Seed | TLC | 22 | 11 | 8 | 31 | 8 | 10 | 2 | 0.5[a] | 1438 |
| | | | also LPC 2, LPE 1. | | | | | | | | |
| *Festuca pratensis* Huds. (Meadow Fescue) | | | | | | | | | | | |
| 2 | Leaf | TLC | 38 | 18 | 19 | 12 | | | 13 | 0.26 | 1679 |
| *Ficus carica* L. (Fig.) | | | | | | | | | | | |
| 2 | Whole fruit (1) | TLC | 18.2 | 3.6 | 45.6 | 4.5 | 4.8 | 7.1 | 1.8 | 0.046 | 1680 |
| | Whole fruit (2) | TLC | 10.5 | 1.9 | 28.3 | 1.9 | 21.9 | 18.4 | 3.0 | 0.022 | 1680 |
| | | | also LPC 2.1, LPE 8.5 (1) and LPC 1.2, LPE 1.8 (2) | | | | | | | | |
| *Fissidens taxifolius* Hedw. (Fissidene Moss) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Flueggea microcarpa* Blume | | | | | | | | | | | |
| 1 | Seed | TLC | 30.2 | 26.4 | 1.0 | 23.6 | | | 18.8 | 0.44 | 1681 |
| *Foeniculum vulgare* Mill. (Fennel) | | | | | | | | | | | |
| 1 | Fruit | TLC | 38.2 | 9.3 | 2.6 | 31.2 | | 7.9 | | 0.3 | 1471 |
| | | | also LPC 3.9, LPE 2.8 | | | | | | | | |
| *Fontinalis antipyretica* Hedw. (Water Moss) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 32.0 | 23.7 | 32.4 | 6.5 | 3.1 | | | 1.67[c] | 1551 |
| *Fragaria* × *ananassa* Duch. | | | | | | | | | | | |
| 10 | Root | TLC | + | + | | + | | | | 0.033-0.051[c] | 1682 |

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*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Fragaria* spp. (Strawberry) | | | | | | | | | | | |
| 1 | Fruit | Frac. pptn. | 0.062 | | | | | | | | 1527 |
| *Fumaria vaillantii* Loisel. (Earthsmoke) | | | | | | | | | | | |
| 1 | Seed | TLC | 64.1 | 4.6 | | 27.5 | | 3.3 | (LPC 0.1) | 0.25 | 1683 |
| *Geum reptans* L. (Creeping Avens) | | | | | | | | | | | |
| 1 | Leaf | TLC | 47 | 23 | 21 | 8 | | | 1 | 0.26 | 1441 |
| *Ginkgo biloba* L. (Ginkgo) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | + | + | | | | | 1684 |
| 1 | Nut, shelled | TLC | 20.8 | 24.5 | 51.2 | | | | | 0.12 | 1685 |
| | | | also LPC 1.6 and LPE 2.4 | | | | | | | | |
| 1 | Leaf[l] | TLC | 1.80 | 0.55 | 0.85 | 0.25 | | | 0.27 | | 1523 |
| *Glaucium fimbrilligerum* Boiss. (Sea Poppy) | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 0.6 | 794 |
| *Gleditsia triacanthos* L. (Honey Locust) | | | | | | | | | | | |
| 1 | Seed oil | TLC | 28 | 24 | | | 23 | | | 8 | 1686 |
| *Glycine max* (L.) Merr. (Soybean) | | | | | | | | | | | |
| 1 | Seed | TLC | 32 | 20 | 16 | 14 | | | 18 | 2.75[c] | 1524 |
| 1 | Seed | PC | 59.9 | 8.3 | | 8.4 | 4.2 | 6.4 | | | 1687 |
| 1 | Seed | TLC | | | NAPE 2.9 mg/seed | | | | | | 1497 |
| 1 | Seed, meal | HPLC | 45.7 | 25.4 | 1.0 | 21.1 | 4.1 | | 2.6 | | 1688 |
| 1 | –, mitochondria | HPLC | 36.9 | 39.2 | | 15.0 | | | 6.1 | | 1688 |
| 1 | Seed, 20 daf | Distribution among organelles (*not* within each): | | | | | | | | | |
| 1 | –, oleosome (*incl. MGDG and DGDG) | TLC | 15.4 | 29.2 | 1.4* | 24.5 | | | 5.5 | | 1689 |
| 1 | –, endoplastic reticulum | TLC | 6.7 | 6.7 | 0.6* | 3.3 | | | 3.3 | | 1689 |
| 1 | –, plastid | TLC | 41.7 | 33.7 | 94.9* | 62.1 | | 18.7 | | | 1689 |
| 1 | –, mitochondria | TLC | 27.3 | 22.1 | 2.6* | 9.9 | | | 70.3 | | 1689 |
| 1 | –, peroxisome | TLC | 8.9 | 8.3 | 0.5* | 0.2 | | | 2.2 | | 1689 |
| 1 | Seed, hypocotyl | TLC | 41 | 20 | 2 | 16 | Trace | 2 | (LPC 3, LPE 2) | | 1690 |
| 1 | –, cotyledon | TLC | 47 | 26 | 1 | 15 | Trace | 2 | (LPC 2, LPE trace) | | 1690 |
| 3 | Seed, coat | TLC | | | + | | | + | + | | 1691 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 45.3-51.7 | 18.0-23.3 | | 12.5-14.4 | | | | | |
| 3 | –, cotyledon | TLC | 45.9-49.3 | 20.6-27.6 | + | 17.3-21.5 | | + | + | | 1691 |
| 3 | –, axis | TLC | 45.2-47.3 | 22.8-27.3 | + | 15.2-17.3 | | + | + | | 1691 |
| 1 | Mixed bean, mature | TLC | 39.0 | 23.3 | | 20.3 | | 4.8 | | 4.87[a] | 1692 |
| 1 | Bean | TLC | 37.5 | 18.8 | 2.5 | 13.8 | | | (NAPE 6.2) | 1.31 | 1693 |
| 1 | –, immature | TLC | | | | | | (DPA 0.039%) | | | 1694 |
| 1 | –, lipid bodies | TLC | 56.7 | 13.4 | 3.4 | 15.5 | | 10.3 | 0 | 0.97 | 1695 |
| 1 | –, protein bodies | TLC | + | + | + | + | | | + (NAPE +) | 2.08[c] | 1696 |
| 1 | Seed, black | TLC | 50.5 | 29.6 | | 10.7 | 9.2 | | | 2.14[c] | 1697 |
| 1 | Leaf | TLC | | 26 | 28 (incl. PC) | | | | 36 | 2.60[l] | 1698 |
| 2 | Root (1) *Incl. PS | TLC | 43.1 | 33.1* | 7.0 | 7.8 | | 3.9 | 5.1 | | 1699 |
| | Root (2) | | 46.4 | 33.3* | 4.9 | 5.8 | | 3.0 | 3.2 | | 1699 |
| 1 | –, microsomes | TLC | 46 | 31 | 2 | 8 | | 2 | (LPE 12) | | 1699 |
| 1 | –, plasma membrane vesicles | TLC | 42.3 | 32.1 | 1.7 | 7.5 | 6.1 | 8.9 | 0.2 | | 1700 |
| 1 | –, mature (NAPE 0.5) | TLC | 46.1 | 31.0 | 2.1 | 23.8 | | 0.6 | 2.7 | 7.9[o] | 1701 |
| 1 | –, immature (NAPE 2.7) | TLC | 30.4 | 26.0 | 5.1 | 24.5 | | 2.5 | 8.8 | 15.2[o] | 1701 |
| 1 | Cotyl, spherosomes | TLC | 67.5 | 20.0 | | 5.9 | | 6.6 | | | 1702 |
| *Goebelia pachycarpa* (C.A. Mey) Bunge | | | | | | | | | | | |
| 1 | Seed | TLC | 41.7 also NAPE 4.1, NALPE 5.5, LPC 5.1 | 18.0 | | 25.6 | | | | 1.5[c] | 1703 |
| *Gossypium arboreum* L. (Tree Cotton) | | | | | | | | | | | |
| 1 | Seed | TLC | 48.0 | 8.8 | | 11.6 | 10.1 | (LPC 15.2) | | | 1704 |

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*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Gossypium arboreum* L. ssp. *indicum* | | | | | | | | | | | |
| 1 | Leaf | TLC | 48.4 | 7.0 | 13.3 | | | | | 0.58[c] | 1494 |
| 1 | Root | TLC | 49.0 | 42.9 | Trace | | | | | 0.27[c] | 1494 |
| *Gossypium aridum* (Rose and Standl.) Skovst. (American Wild Cotton) | | | | | | | | | | | |
| 1 | Seed | TLC | 31.3 | 12.5 | | 5.2 | 18.9 | (LPC 5.8) | | | 1704 |
| *Gossypium armorianum* Kearn. | | | | | | | | | | | |
| 1 | Seed | TLC | 36.0 | 15.5 | | 7.4 | 18.2 | (LPC 6.0) | | | 1704 |
| *Gossypium barbadense* L. (Sea Island Cotton) | | | | | | | | | | | |
| 1 | Seed | TLC | 38.2 | 10.9 | | 13.9 | 11.8 | (LPC 12.6) | | 0.39 | 1705 |
| | | | The PC contains traces of malvalic acid in the 2-position | | | | | | | | 1706 |
| 1 | Seed, kernel | TLC | 28.2 | 17.9 | | 11.7 | 14.2 | (LPC 13.1) | | 2.38 | 1707 |
| 1 | Seed, kernel | TLC | 50.4 | 14.1 | | 20.4 | | (LPC 5.6) | | 1.6[c] | 1708,1709 |
| 1 | Leaf | TLC | + | 0 | + | + | | + | + | | 1710 |
| *Gossypium davidsonii* Kellogg | | | | | | | | | | | |
| 1 | Seed | TLC | 32.4 | 16.0 | | 4.9 | 16.2 | (LPC 4.5) | | | 1704 |
| *Gossypium gossypioides* (Ulbr.) Stanley | | | | | | | | | | | |
| 1 | Seed | TLC | 23.4 | 14.3 | | 9.6 | 13.5 | (LPC 9.7) | | | 1704 |
| *Gossypium herbaceum* L. (Levant Cotton) | | | | | | | | | | | |
| 1 | Seed | TLC | 41.9 | 7.1 | | 13.5 | 13.4 | (LPC 16.9) | | | 1704 |
| *Gossypium hirsutum* L. (Upland Cotton) | | | | | | | | | | | |
| 1 | Seed, glanded | TLC | 36.9 | 21.8 | | 10.6 | 14.3 | (LPC 7.7) | | | 1704 |
| 1 | Seed | TLC | | | | | | 0.3 | (LPI 0.1) | | 1711 |
| 1 | Seed | TLC | | NAPE 4.1, NALPE 3.3 | | | | | | | 1712 |
| 3 | Seed | TLC | | NAPE +, NALPE +, LPC + | | | | | | | 1713 |
| 1 | –, kernel | TLC | 50.2 | 13.4 | | 26.6 | | | | 1.5[c] | 1374,1714 |
| 1 | –, oil body | TLC | 58.6 | 4.6 | | 18.1 | 18.7 | | | 1.18 | 1482 |
| 3 | Leaf | TLC | 47.8-48.8 | 0 | 19.2-23.6 | 8.4-11.2 | | 2.5-4.4 | | | 1710 |
| 1 | Bud[a] | TLC | 30.4 | 2.6 | | 11.5 | | | | | 1715 |
| 1 | Bud | TLC | 41.3 | 8.0 | | 9.5 | | 21.2 | | | 1716 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 48-h seedling, cotyledon | | | | | | | | | |
| 1 | –, lipid bodies | TLC | 35 | 21 | 0 | 34 | 4 | 0 | | 1717 |
| 1 | –, mitochondria | TLC | 35 | 32 | 1 | 5 | 0 | 20 | | 1717 |
| 1 | –, glyoxysomes | TLC | 49 | 12 | 13 | 15 | 0 | 0 | | 1717 |
| 1 | Flower, 1st day | TLC | 42.7 | 10.9 | | 10.4 | 6.2 | | | 1716 |
| 1 | Boll | TLC | 35.4 | 8.8 | | 13.1 | 19.1 | | | 1716 |
| 1 | Bark | TLC | 28.5 | 17.4 | | 10.6 | 28.9 | | | 1716 |
| 1 | Stem | TLC | 17.7 | 18.1 | | 13.0 | 37.4 | | | 1716 |
| 1 | Root | TLC | 38.7 | 2.6 | | 10.5 | 35.2 | | | 1716 |
| 1 | Extrafloral nectar | TLC | 44.3 | 4.4 | | 9.6 | (LPC 21.3, LPE 12.7) | | | 1718 |
| 1 | Fiber, immature | TLC | 47.8 | 30.4 | 7.0 | | 14.7 | | | 1719 |
| 1 | –, mature | TLC | 56.6 | | | | 43.6 | | | 1719 |
| *Gossypium hirsutum* L., glandless | | | | | | | | | | |
| 3 | Leaf | TLC | 30.3-39.7 | + | 21.3-24.4 | 10.7-12.0 | 1.9-3.9 | | | 1710 |
| 1 | Leaf | TLC | 37.5 | 20.1 | | 10.9 | 20.0 | | | 1704 |
| 1 | Seedling | TLC | NAPE in leaf 2.5, stem 3.2, plumule 3.2, cotyledon 1.9, root 3.8 | | | | | | | 1720 |
| *Gossypium klotzschianum* Anderss. | | | | | | | | | | |
| 1 | Seed | TLC | 33.4 | 17.2 | | 6.1 | 14.6 | (LPC 6.4) | | 1704 |
| *Gossypium raimondii* Ulbr. | | | | | | | | | | |
| 1 | Seed | TLC | 34.5 | 15.9 | | 5.8 | 16.9 | (LPC 5.8) | | 1704 |
| *Gossypium thurberi* Todaro (Thurber's Cotton) | | | | | | | | | | |
| 1 | Seed | TLC | 34.0 | 14.0 | | 4.7 | 22.5 | (LPC 5.7) | | 1704 |
| *Grimmia pulvinata* (Hedw.) Sm. | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | 1436 |
| *Halocnemum strobilaceum* (Pall.) M. Bieb. | | | | | | | | | | |
| 1 | Shoot | TLC | 40.6 | 16.8 | 11.1 | 8.0 | | 19.1 | 0.261[c] | 1488 |
| *Hancornia speciosa* Müll Arg. (Mangaba Tree) | | | | | | | | | | |
| 1 | Latex[e,s] | Extn. | 0.08 | | | | | | | 1721 |
| *Hedychium gardnerianum* Ker-Gawl. (Kahili Ginger) | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.53 | | | | | 1402 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Helianthus annuus* L. (Sunflower) | | | | | | | | | | | |
| 1 | Seed | TLC | 35.2 | 13.0 (incl. PG) | | 24.3 | | 13.0 | 14.6 | 2.5 | 1722 |
| 1 | Seed, dehulled | TLC | 56.2 | 11.7 | 4.3 | 7.4 | 1.8 | 4.3 | (LPC trace) | 200[k] | 1723 |
| 2 | Achene, dehulled | TLC | | + (fatty acid distribution given) | | | | | | | 1724 |
| 1 | Seed, oil | HPLC | 47.6 | 20.9 | | 19.7 | | 11.8 | | | 1725 |
| 1 | Seed cotyledon, oleosome[g] | TLC | 79 | 13 | | 8 | 0 | | | | 1571 |
| 1 | –, microsome[g] | TLC | 76 | 12 | | 10 | 2 | | | | 1571 |
| 1 | Hypocotyl, nuclei | TLC | 23.0 | 24.6 | | 10.3 | | 7.4 | 15.6 | 58[a] | 1726 |
| 1 | –, nuclear membrane | TLC | 25.5 | 25.3 | 29.8 | 7.4 | | | | 51.3[a] | 1726 |
| 1 | Stems and petioles | TLC | 39.9 | 27.7 | 12.5 | 17.0 | | 2.9 | | 0.086 | 1638 |
| 1 | Leaf, plasma membrane | TLC | 37 | 33 | 14 | 16 | | 0 | | 540[l] | 1727 |
| 1 | –, chloroplast envelope membrane[a,c] | TLC | 28.9 | 1.8 | 5.3 | 0.6 | | | 0 | 36.6 | 1728 |
| 1 | Shoot, 20 days old | TLC | 30.9 | 23.4 | 26.2 | 19.4 | | | | 0.24[c] | 1729 |
| 1 | Pollen[l] | TLC | 9.1 | 4.3 | | 0.5 | | (LPC 0.4, LPE 0.5) | | | 1730 |
| 1 | Root | TLC | 51.3 | 25.9 | | 12.3 | | 10.5 | | | 1731 |
| 1 | –, microsome | TLC | 44.4 | 33.8 | | 12.7 | | 9.1 | | | 1731 |
| *Helianthus tuberosus* L. (Jerusalem Artichoke) | | | | | | | | | | | |
| 1 | Tuber, plasma membrane | TLC | 39.3 | 43.6 | 2.6 | 10.6 (incl. PS) | | 3.9 | | 1.52[h] | 1732 |
| *Heliotropium lasiocarpum* F and M (Heliotrope) | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 0.3 | 794 |
| *Helodium blandowi* (Web. et Mokr.) Warnst. | | | | | | | | | | | |
| 1 | Whole plant | TLC | 26.8 | 20.8 | 27.8 | 8.4 | 9.5 | | | 0.52[c] | 1493 |
| *Heracleum angustisectum* Recn. | | | | | | | | | | | |
| 1 | Seed | TLC | 37 | 10 | | 29 | | 11 | | 1.5[a] | 1438 |
| | | | also LPC 6, LPE 6. | | | | | | | | |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Heracleum lehmannianum* Bunge (Cow Parsnip, Mandan) | | | | | | | | | | | |
| 1 | Seed | TLC | 30.4 | 19.5 | 2.8 | 24.8 | | | | | 1733 |
| | | | also LPC 2.4, LPI 1.8, NAPE 12.2, NALPE 6.1 | | | | | | | | |
| *Heracleum sibiricum* L. | | | | | | | | | | | |
| 1 | Seed | TLC | 42 | 14 | 2 | 18 | 1 | 14 | 2 | 4.4[a] | 1438 |
| | | | also LPC 3, LPE 4. | | | | | | | | |
| *Heracleum ternatum* L. | | | | | | | | | | | |
| 1 | Seed | TLC | 44 | 11 | 2 | 30 | | 6 | | 1.2[a] | 1438 |
| | | | also LPC 3, LPE 4. | | | | | | | | |
| *Hevea brasiliensis* (Willd.) Mill. (Pará Rubber) | | | | | | | | | | | |
| 1 | Mature tree, latex | TLC | 58.4 | 21.0 | | 20.6 | | | | 0.23 | 1734 |
| 1 | Seedling, latex[a] | Frac. pptn. | 51 | 3 | | 10.5 | | 0 | | 0.71 | 1735 |
| *Hibiscus cannabinus* L. (Kenaf) | | | | | | | | | | | |
| 9 | Seed | TLC | 13.3-38.0 | 8.5-29.7 | 4.4-19.7 | 1.3-5.2 | 1.0-6.5 | 1.0-14.1 | 1.0-6.3 | 3.91-10.9[a] | 1736 |
| | | | also LPC 1.1-7.5 | | | | | | | | |
| 2 | Seed (1) | TLC | 38.4 | 25.1 | | 22.0 | | | | | 1737 |
| | Seed (2) | | 39.6 | 23.7 | | 21.8 | | | | | |
| | | | also NAPE 7.1, NALPE 3.6, LPC 2.3, LPI 1.5 (1), and NAPE 8.0, NALPE 3.1, LPC 2.6, LPI 1.2 (2) | | | | | | | | |
| 1 | Seed | TLC | 38.2 | 15.6 | | 22.7 | | | | 1.0[c] | 793,1377 |
| 1 | Bud | TLC | 30.0 | 15.3 | 9.7 | 27.2 | | 7.4 | | 0.41[c] | 1738 |
| | | | also NAPE 7.7, NALPE 2.7 | | | | | | | | |
| 1 | Flower | TLC | 30.4 | 15.2 | 8.5 | 30.0 | | 5.8 | | 0.32[c] | 1738 |
| | | | also NAPE 7.0, NALPE 3.1 | | | | | | | | |
| 1 | Leaf | TLC | 23.1 | 16.0 | 11.4 | 25.0 | | 13.5 | | 0.40[c] | 1738 |
| | | | also NAPE 7.8, NALPE 3.2 | | | | | | | | |
| 1 | Stem | TLC | 23.7 | 15.0 | 15.0 | 25.2 | | 12.6 | | 0.20[c] | 1738 |
| | | | also NAPE 6.2, NALPE 2.3 | | | | | | | | |
| 1 | Root | TLC | 26.5 | 16.1 | 15.7 | 31.8 | | 0 | | 0.33[c] | 1738 |
| | | | also NAPE 7.5, NALPE 2.4 | | | | | | | | |
| *Hibiscus sabdariffa* L. (Roselle) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | + | + | + | + | + | 1.7 | 1457 |
| | | | also LPC +, LPE +, NALPE +. | | | | | | | | |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Hippophaë rhamnoides* L. (Sea Buckthorn) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | + | + | | | | 0.6 | 1739 |
| | | | also NAPE +, NALPE +, LPC +, LPI + | | | | | | | | |
| 1 | Leaf | TLC | 32.8 | 29.7 | 21.5 | 16.0 | | | | 12.1[a] | 1740 |
| 1 | Fruit pulp | TLC | 26.7 | 13.1 | | 8.9 | 5.8 | | | 0.2-0.5[a] | 1741 |
| *Hordeum distichon* L. (Two-Rowed Barley) | | | | | | | | | | | |
| 1 | Leaf, plastid[l] | TLC | | | 0.13 | | | | | | 1742 |
| *Hordeum vulgare* L. (Barley) | | | | | | | | | | | |
| 2 | Whole grain (1) | TLC | 44.4 | 8.8 | 0.2 | 1.3 | 4.8 | Trace | 1.5 | 0.56 | 1743 |
| | Whole grain (2) | | 44.3 | 7.6 | 0.8 | 1.1 | 5.0 | 0.2 | 1.7 | 0.58 | |
| | | | also LPC 37.3 (1) and 36.8 (2) | | | | | | | | |
| 3 | Grain | TLC | 39.8- | 9.9- | 3.1- | 4.1-5.3 | | | 6.2-7.0 | 0.030- | 1744 |
| | *Incl. PS | | 41.8* | 10.8 | 4.1 | | | | | 0.059 | |
| | | | also LPC 28.5-31.2 | | | | | | | | |
| 1 | Starch, free | TLC | 12.1* | 4.9 | 8.3 | 3.5 | (LPC 30.8) | | 40.4 | 0.0008[c] | 1745 |
| | *Incl. PS | | | | | | | | | | |
| 1 | –, bound | TLC | 21.2* | 3.4 | 7.1 | 2.2 | (LPC 26.8) | | 39.3 | 0.055[c] | 1745 |
| | *Incl. PS | | | | | | | | | | |
| 1 | Leaf | PC | 52 | 1.4 | 22.6 | 14.0 | | | | | 1746 |
| 1 | Leaf | TLC | 36.9 | 15.4 | 30.8 | 7.2 | | 0 | 1.8 | 0.76[o] | 1747 |
| 1 | –, thylakoid[a] | TLC | 4.3 | | 10.8 | | | | | 3.69[i] | 1748 |
| 1 | –, PS(II) vesicles[a] | TLC | 0 | | 5.1 | | | | | 2.36[i] | 1748 |
| 1 | –, PS(I) vesicles[a] | TLC | 0 | | 6.2 | | | | | 4.65[i] | 1748 |
| 1 | –, tonoplast | TLC | 67.0 | 12.0 | 6.2 | 9.6 | 5.3 | | | | 1749 |
| 1 | –, plasma membrane | TLC | 47.1 | 30.5 | 3.6 | | | 11.8 | | 0.08[a] | 1750 |
| 1 | –, intracellular membrane | TLC | 47.0 | 16.5 | 17.3 | | | 9.0 | | 1.86[a] | 1750 |
| 1 | –, chloroplast[a] | TLC | | | 11 | | | | | | 1489 |
| 1 | Caryopsis, aleurone protoplast | TLC | 0 | + | | + | | + | (LPC +, LPE +) | | 1751 |
| 1 | –, lipid bodies | TLC | 0 | 0 | | + | | + | | | 1751 |
| | | | also NAPE +, NALPE +, LPC + and LPI +. | | | | | | | | |
| 1 | Seedling, 7 days[l] | TLC | 1.3 | 0.83 | 0.60 | 0.41 | 0.35 | | | | 1752 |
| 1 | –, mesophyll protoplast | TLC | + | 0 | | + | | | | | 1751 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | also NAPE +, NALPE +, LPC +, LPE + and LPG +. | | | | | | | | |
| 1 | Root *Incl. PS | TLC | 50.6 | 36.5* | 5.2 | Trace | | 2.4 | 4.7 | | 1699 |
| 1 | –, endoplastic reticulum †incl. LPE | TLC | 59.5 | 20.6 | 6.9 | 9.8† | 1.5 | 1.0 | 0.1 | (LPC 0.7) | 1753 |
| 1 | –, tonoplast and Golgi membrane | TLC | 57.6 | 23.2 | 6.3 | 7.4† | 2.5 | 1.8 | 0.6 | (LPC 0.6) | 1753 |
| 1 | –, plasma membrane | TLC | 42.7 | 33.8 | 3.6 | 5.1† | 6.6 | 5.6 | 1.7 | (LPC 0.8) | 1753 |
| *Huperzia selago* (L.) Bernh. (Fir Clubmoss) | | | | | | | | | | | |
| 1 | whole plant | TLC | + | + | | | | | | | 1436 |
| *Hyacinthus* spp. (Hyacynth) | | | | | | | | | | | |
| 1 | Leaf | TLC | | | 8 | | | | | | 1440 |
| *Hydnocarpus anthelminticus* Pierre (Chaulmoogra Tree) | | | | | | | | | | | |
| 1 | Leaf | TLC | ++ | + | + | + | | + | | | 1552 |
| *Hygrohypnum ochraceum* (Turn. ex Wils.) Loeske | | | | | | | | | | | |
| 1 | Whole plant | TLC | 32.5 | 22.8 | 21.4 | 7.0 | 9.6 | | | 0.23 | 1493 |
| *Hylocomium splendens* (Lesq. and James) Lindl. | | | | | | | | | | | |
| 1 | Gametophore | TLC | 67 | 13 | 7 | 13 | | | | 15[a] | 1754 |
| *Hypnum cupressiforme* Hedw. (Hypnum Moss) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Ilex aquifolium* L. (English Holly) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | + | + | | | + | | 1755 |
| *Illicium verum* Hook. f. (Star Anise) | | | | | | | | | | | |
| 1 | Seed, dehusked | TLC | 19.5 | | 3.3 | 11.3 | 12.7 | | ($Me_2$N-PE 2.1) | 0.067 | 1669 |
| *Impatiens balsamina* L. (Garden Balsam) | | | | | | | | | | | |
| 1 | Leaf | TLC | 35.1 | 25.5 | 31.5 | 6.3 | 1.6 | | | 1480[q] | 1756 |
| 1 | –, chloroplast | TLC | 25 | + | 67 | 8 | | | | 1220[q] | 1756 |
| *Indigofera enualphylla* (Indigo) | | | | | | | | | | | |
| 1 | Seed | TLC | 37.5 | 25.7 | | 29.7 | | | 8.7 | 0.16[c] | 1757 |
| | | | also LPC 0.4 and LPE 0.3 | | | | | | | | |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Indigofera glandulosa* J. C. Wendl. | | | | | | | | | | | |
| 1 | Seed | CC (silica) | 41.2 | 58.8 | | | | | | | 1576 |
| *Indigofera hirsuta* L. (Hairy Indigo) | | | | | | | | | | | |
| 1 | Seed | CC(silica) | 34.4 | 65.6 | | | | | | | 1576 |
| *Indigofera trifoliata* L. (Three-Leaf Indigo) | | | | | | | | | | | |
| 1 | Seed | CC(silica) | 38.4 | 66.6 | | | | | | | 1576 |
| *Ipomoea aquatica* Forssk. (Swamp Cabbage) | | | | | | | | | | | |
| 1 | Seed | TLC | 48.4 | 27.1 | | 20.9 (incl. PS) | | 2.8 | | 0.42 | 1577 |
| *Ipomoea batatas* (L.) Lam. (Sweet Potato) | | | | | | | | | | | |
| 1 | Leaf | TLC | | | 0.21[l] | | | | | | 1402 |
| 1 | Leaf | TLC | + | + | + | + | | | | | 1631 |
| 1 | Root, peeled and cured | TLC | 26 | 29 | 4 | 19 | 4 | 1.5 | 5.9 | 0.73[c] | 1758 |
| 9 | Tuber | CC (Florisil) | 28.9-39.0 | 61.0-71.1 | | | | | | 0.11-0.31 | 1759 |
| 1 | Tuber mitochondrial membrane | TLC | 33.2 | 38.7 | | | | (LPC 6.6) | | | 1760 |
| *Iris* spp. (Iris) | | | | | | | | | | | |
| 1 | Leaf | TLC | | | 9 | | | | | | 1440 |
| *Irvingia gabonensis* Baill. (Ogbono) | | | | | | | | | | | |
| 1 | Seed | TLC | 47 | 4 | 15 | 15 | | | 19 | 3.49[c] | 1524 |
| *Ixora parviflora* Vahl (Torch Tree) | | | | | | | | | | | |
| 1 | Seed | TLC | 29.1 | 26.2 | 3.1 | 24.5 | | | 17.1 | 0.70 | 1681 |
| *Juglans regia* L. (English Walnut) | | | | | | | | | | | |
| 1 | Nut | TLC | 12.5 | 19.0 | 0 | 0 | | 13.0 | (LPE 4.5) | 1.8[a] | 1480 |
| 1 | Nut[g] | Choline | 21 | 31 | | | | | | 1.8 | 1480 |
| *Kalanchoë daigremontiana* Ham. and Perr. (Devil's Backbone) | | | | | | | | | | | |
| 1 | Leaf | TLC | | | | | + | | | | 1450 |
| 1 | Leaf, tonoplast | TLC | 37.6 | 36.1 | 12.9 | | 3.3 | 10.0 | | | 1749 |
| *Lablab purpureus* (L.) Sweet (Hyacinth Bean) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | | | | (LPC +) | | 1428 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Lactuca sativa* L. (Lettuce) | | | | | | | | | | | |
| 1 | Leaf[l] | Choline | 2 | | | | | | | | 1451 |
| [l]1 | Leaf | TLC | 33.2 | 7.5 | 42.0 | 6.4 | 3.4 | 3.2 | 4.3 | 0.037 | 1761 |
| 1 | –, thylakoid | TLC | | | 12.0[a] | | | | | | 1762 |
| 1 | –, chloroplast | TLC | + | + | ++ | + | | + | | | 1396 |
| 1 | Stalk | TLC | ++ | + | + | ++ | | + | | | 1396 |
| *Lactuca sativa* L. ssp. *asparagina* Bail. (Celtuce) | | | | | | | | | | | |
| 1 | Leaf | TLC | 12.2 | 61.2 | 26.6 | | | | | 0.413 | 1446 |
| 1 | Shoot | TLC | 61.3 | 4.4 | 16.1 | | | 10.9 | (LPC 17.3) | 0.204 | 1446 |
| *Lantana camara* L. ssp. *aculeata* (Yellow Sage) | | | | | | | | | | | |
| 1 | Stems and petioles | TLC | 40.3 | 25.1 | 13.0 | 17.6 | | 4.0 | | 0.181 | 1638 |
| *Larix sibirica* Ledeb. (Siberian Larch) | | | | | | | | | | | |
| 1 | Cambium | TLC | 48 | 21 | | 0 | 5 | 16 | (NAPE 9) | 0.56 | 1763 |
| *Lathyrus sativus* L. (Grass Pea) | | | | | | | | | | | |
| 1 | Seed | CC (silica) | + | 65.8 | | | | | | | 1764 |
| *Lavandula latifolia* Medic. (Broadleaved Lavender) | | | | | | | | | | | |
| 1 | Root<br>*Incl. PS | TLC | 52.1 | 35.5* | 5.0 | Trace | | 3.3 | 3.5 | | 1699 |
| *Lavandula vera* DC (English Lavender) | | | | | | | | | | | |
| 1 | Cell Culture | TLC | 43 | 48 | | 1 | Trace | 3 | | | 1765 |
| *Lemna minor* L. (Lesser Duckweed) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 41.0 | 24.1 | 10.2 | 10.8 | 3.1 | 2.6 | 8.2 | 3.52[c] | 1445 |
| 1 | Chloroplast | TLC | 18 | | 73 | 9 | | | | 1372[q] | 1766 |
| 1 | Frond | TLC | 30 | 16 | 9 | 6 | 3 (incl. PA, LPC, LPE) | | | 0.071 | 1767 |
| *Lemna trisulca* L. (Star Duckweed) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 35.5 | 20.2 | 16.1 | 7.8 | 3.5 | 7.8 | 9.1 | 2.42[c] | 1445 |
| *Lepidium sativum* L. (Garden Cress) | | | | | | | | | | | |
| 1 | Seed | TLC | 33.5 | 29.7 | 4.0 | 26.0 | | | 6.8 | 0.80[c] | 1429 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]µmol PL/mg protein; [i]µmol PL/mg chlorophyll; [j]µg PL/mg protein; [k]µg lipid P/g; [l]µmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]µmol PL/g dwb; [p]µg PL/100 mg fwb; [q]µg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]µmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]µg PL/mL; [x]µg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]µg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]µg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Lespedeza bicolor* Turcz. (Bush Clover) | | | | | | | | | | | |
| 1 | Seed | TLC | 36.5 | 17.3 | | 21.5 | | | | 4.99[a] | 1768 |
| *Levisticum officinale* Koch (Lovage) | | | | | | | | | | | |
| 1 | Seed | TLC | 17 | 6 | | 25 | | 47 | | 1.1[a] | 1438 |
| | | | also LPC 3, LPE 2 | | | | | | | | |
| 1 | Leaf? | TLC | 37.2 | 2.8 | | 2.6 | 0.1 | 1.2 | 43.9 | | 1472 |
| *Lilium longiflorum* Thumb. (Trumpet Lily) | | | | | | | | | | | |
| 1 | Pollen | TLC | 49[H] | 27[H] | + | 11[H] | + | | | 0.56 | 1769 |
| *Limnanthes alba* Hart. ex Benth. (Meadowfoam) | | | | | | | | | | | |
| 1 | Seed, cotyledon, 10 dap[a] | TLC | 35 | 40 | | | | 11 | | | 1770 |
| v1 | –, 60 dap[a] | TLC | 3 | 1 | | | | <1 | | | 1770 |
| *Limnobium spongia* (Bosc) Steud. (Frogbit) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 37.5 | 25.0 | 12.1 | 5.6 | 2.8 | 13.6 | 3.4 | 2.90[c] | 1445 |
| *Lindelofia macrostyla* (Bunge) Pop. | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 0.3 | 794 |
| *Lindelofia tschimganica* (Lipsky) Pop. ex Pazij. | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 1.2 | 794 |
| *Linum usitatissimum* L. (Linseed, Flax) | | | | | | | | | | | |
| 1 | Seed[p] | TLC | 155 | 220 (incl. PS) | | 2 | (LPC 67) | | | | 1771 |
| 1 | Seed, cotyledon | TLC | 58.0 | + | | + | | | | | 1772 |
| 1 | –, oil body | TLC | 57.2 | 2.8 | | 6.9 | 33.1 | | | 0.90 | 1482 |
| 1 | –, microsomes | TLC | 60.6 | 10.6 | 0 | 21.4 | | 7.5 | | | 1570 |
| *Lolium cuneatum* Nevski (Poison Ryegrass) | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 0.3 | 794 |
| *Lolium perenne* L. (Perennial Ryegrass) | | | | | | | | | | | |
| 1 | Leaf | TLC | 44 | 18 | 25 | 7 | | | 7 | 3.05[l] | 1523 |
| *Luffa aegyptiaca* Mill. (Sponge Gourd) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | + | + | | | | | 1631 |
| *Lupinus albus* L. (White Lupine) | | | | | | | | | | | |
| 1 | Seed[e] | Frac. pptn. | 0.411 | 0.123 | | | | | | | 718 |
| 1 | Leaf | TLC | 53.1 | 23.4 | 17.9 | | | 5.5 | | 1.62 | 1773 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2 | –, thylakoid | TLC | | 250-330[q] | | | | | | | 1774 |
| 1 | Root<br>*Incl. PS | TLC | 35.2 | 36.2* | 6.7 | 8.1 | | 8.0 | 5.1 | | 1699 |
| *Lupinus arboreus* Sims. (Tree Lupine) | | | | | | | | | | | |
| 1 | Pollen | TLC | + | + | | + | | | | | 1603 |
| *Lupinus luteus* L. (Yellow Lupine) | | | | | | | | | | | |
| 1 | Root | TLC | 36.7 | 23.6 | 7.1 | 8.8 | 9.0 | 10.8 | 4.0 | | 1775 |
| 1 | –, mitochondria<br>*Incl. PS | TLC | 32.8 | 23.7 | 12.9* | 12.7 | | 9.0 | 9.0 | 72.5[a] | 1776 |
| 1 | –, microsomes<br>*Incl. PS | TLC | 34.9 | 28.2 | 9.5* | 14.1 | | 5.8 | 7.5 | 71.5[a] | 1776 |
| *Lycopersicon esculentum* Mill. (Tomato) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | + | | Trace | (LPC +) | 0.4 | 1777 |
| 1 | Leaf | PC | 35 | 1.5 | 23 | 21 | | | | | 1746 |
| 1 | Leaf | TLC | 50 | 21 | 20 | 5 | | | 5 | 2.18[l] | 1523 |
| 1 | Leaflet | TLC | 8.8 | 6.4 | 16.1 | 12.0 | | 56.6 | | | 1778 |
| 2 | Fruit[l] | Choline | 8-19 | | | | | | | | 1451 |
| 1 | Fruit | TLC | 43.2 | 23.5 | | 10.4 | 4.5 | 9.6 | 8.7 | 0.152 | 1779 |
| 1 | –, microsomes | TLC | 53.7<br>also LPC 1.7 and LPE 2.4 | 31.0 | 2.6 | 6.8 | | 1.8 | | | 1780 |
| 1 | –, crude plastid | TLC | 40.2<br>also LPC 1.4 and LPE 2.8 | 27.1 | 12.8 | 8.2 | | 5.7 | 1.7 | | 1780 |
| 1 | –, pericarp | TLC | 47.2 | 27.0 | 3.8 | 13.3 | 3.4 | 4.0 | 1.4 | 0.038 | 1781 |
| 1 | –, mitochondria | TLC | 34.1 | 23.7 | 4.3 | 14.2 | 8.0 | 7.3 | 8.2 | | 1781 |
| 1 | –, chloroplast[i] | TLC | 2.83 | 2.68 | 0.48 | | | | | | 1782 |
| 1 | –, chloroplast[i] | TLC | 0.32 | 0.08 | 0.29 | | | | | | 1782 |
| 1 | Leaf, thylakoid[m] | TLC | 0.13 | 0.38 | | | | | | | 1783 |
| 1 | Leaf, thylakoid | TLC | | | 11.4[a] | | | | | | 1762 |
| 1 | Root | TLC | 48.6 | 39.1 | tr | | | | | 1.55[c] | 1494 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]µmol PL/mg protein; [i]µmol PL/mg chlorophyll; [j]µg PL/mg protein; [k]µg lipid P/g; [l]µmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]µmol PL/g dwb; [p]µg PL/100 mg fwb; [q]µg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]µmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]µg PL/mL; [x]µg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]µg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]µg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Lycopersicon esculentum* ssp. *cerasiforme* (Dunal) Alef. (Cherry Tomato) | | | | | | | | | | | |
| 1 | Fruit, outer pericarp | TLC | 25.4 | 27.2 | 9.2 | 10.5 | | 27.7 | | 0.15[c] | 1784 |
| 1 | Callus[k] | TLC | 80.2 | 154.5 | | | | | | | 1785 |
| *Lycopersicon esculentum* ssp. *eupimpinellifolium* (Mill.) Brezh. | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | + | + | | | | | 1786 |
| *Lycopersicon esculentum* ssp. *pruniforme* Brezh. | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | + | + | | | | | 1786 |
| *Lycopersicon hirsutum* Dunal ssp. *glabratum* Mill. (Wild Tomato) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | + | + | | | | | 1786 |
| *Lycopodium annotinum* L. (Stiff Clubmoss) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 4578 |
| *Lycoris incarnata* Comes | | | | | | | | | | | |
| 1 | Flower | TLC | | 1.6 | | | | | | 0.009 | 1787 |
| *Lycoris radiata* Herb. (Red Spiderlily) | | | | | | | | | | | |
| 1 | Flower | TLC | 30.5* | | | | | | | 0.05 | 1788 |
| | | | *16:0/16:0 PC and 16:0/18:2 PC isolated from this fraction by preparative TLC | | | | | | | | 1788 |
| 1 | Leaf | TLC | + | + | + | + | | | | | 1631 |
| *Lysimachia nummularia* L. (Moneywort) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 25.9 | 16.0 | 13.8 | 13.0 | 4.7 | 4.9 | 21.7 | 21.8 | 1789 |
| *Macrozamia communis* L. | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | | | | | | | 1436 |
| *Magnolia denudata* Desr. (Yulan) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | | | | | | | 1436 |
| *Malabajla graveolens* L. | | | | | | | | | | | |
| 1 | Seed | TLC | 32 | 9 | | 42 | | 11 | 2 | 2.0[a] | 1438 |
| | | | also LPC 4 | | | | | | | | |
| *Malus domestica* Borkh. (Apple) | | | | | | | | | | | |
| 1 | Seed | TLC | 30.8 | 16.0 | 1.8 | 28.4 | 2.5 | 10.7 | 1.1 | 0.2 | 1639 |
| | | | also LPC 3.6, LPE 2.1 | | | | | | | | |
| 1 | Leaf | TLC | 41.6 | 21.8 | 19.6 | 17.0 | | | | 0.36 | 1790 |
| 1 | Stem | TLC | 42.0 | 32.2 | 7.7 | 18.2 | | | | 0.14 | 1790 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Shoot, xylem | TLC | 54.5 | 20.1 | 6.3 | 19.0 | | | | 0.027[c] | 1791 |
| 1 | –, phloem | TLC | 63.2 | 18.7 | 6.6 | 11.5 | | | | 0.076[c] | 1791 |
| 1 | Fruit, peeled and cored, preclimacteric[a] | TLC | 21.5 | 14.4 | 3.1 | 6.0 | 0.4 | 0.3 | 0.7 | 46.6 | 1792 |
| 1 | –, postclimacteric | TLC | 22.7 | 10.7 | 0.8 | 6.2 | 0.4 | 0.7 | 0.5 | 42.2 | 1792 |
| 2 | –, mitochondria | TLC | 9.2-16.1 | 21.8-64.6 | 4.3-5.6 | 2.0-2.9 | 7.6 | 2.5-3.8 | 5.0-6.1 | 52.5-63.1[a] | 1793 |
| 1 | –, parenchyma | TLC | 35.2 | 41.6 | Trace | 3.2 | Trace | 16.8 | 3.2 | | 1794 |
| 1 | –, epidermis | TLC | 33.8 | 18.2 | 9.5 | 18.2 | Trace | 11.6 | 8.7 | | 1794 |
| 1 | Fruit | TLC | 34.9 | 0.6 | | 14.6 | | 19.1 | (LPC 20.0, LPE 10.9) | | 1795 |
| 1 | –, callus culture | TLC | Trace | 44.2 | 32.4 | 0.7 | | 12.4 | (LPC 8.1, LPE 2.2) | | 1795 |
| 1 | Bud, dormant | TLC | 40 | 37 | 8 | 15 | | <1 | | | 1796 |
| 1 | Root | TLC | 23.5 | 47.0 | 12.2 | 17.4 | | | | 0.12 | 1790 |
| *Malus sylvestris* Mill. (Crabapple) | | | | | | | | | | | |
| 1 | Bark | TLC | 4.7 | 45.2 | 18.4 | 4.4 | | (LPC 27.3) | | 0.429 | 1797 |
| *Mandragora turcomanica* Mizger. (Mandrake) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | + | | + | | 0.687 | 1798 |
| 1 | Fruit, flesh | TLC | + | + | | + | | + | | 0.067 | 1798 |
| *Mangifera indica* L. (Mango) | | | | | | | | | | | |
| 3 | Seed | TLC | 24.3-25.5 | 17.8-19.1 | | | | (LPC 16.5-18.0) | | | 1799 |
| 10 | Kernel | TLC | + | + | | | + Trace | + | (LPC +) | 0.1-0.8[a] | 1800 |
| 1 | Kernel, decorticated | TLC | 20.5 | 13.2 | 13.7 | 15.5 | | (LPE 11.2) | | 0.12[c] | 1801 |
| *Manihot esculenta* Crantz (Cassava) | | | | | | | | | | | |
| 1 | Leaf, young | TLC | Trace | 35.9 | 46.0 | 8.8 | | 1.5 | 7.9 | 1.46 | 1802 |
| 1 | Root, decorticated | TLC | 37.6 | 21.5 | 3.1 | 20.3 | 1.9 | 12.7 | 2.9 | 0.706[l] | 1803 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Marchantia berteroana* Lehm. and Lindenb. | | | | | | | | | | | |
| 1 | Thallus | TLC | 27 | 14 | 24 | 11 | | | 24 | 0.66[l] | 1523 |
| *Marchantia polymorpha* L. | | | | | | | | | | | |
| 1 | Whole plant *Incl. LPE | TLC | 21.6 | 21.6 | 18.3 | 13* | 13.8 | | | 0.94[c] | 1492 |
| *Matricaria chamomila* L. (Sweet False Camomile) | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 1.1 | 794 |
| *Medicago sativa* L. (Alfalfa, Lucerne) | | | | | | | | | | | |
| 1 | Leaf | TLC | 27 | 18 | 24 | 10 | | | 21 | 2.78[l] | 1523 |
| 1 | Leaf | HPLC | + | + | + | + | | | | | 1804 |
| 3 | –, chloroplast | TLC | 29-38 | | 55-62 | 5-12 | | | | | 1805 |
| 1 | Stems and petioles | TLC | 42.3 | 27.2 | 9.8 | 17.4 | | 3.3 | | 0.20 | 1638 |
| *Melilotus alba* Desr. (White Sweet Clover) | | | | | | | | | | | |
| 1 | Leaf | PC | 30.0 | 8.4 | 24.9 | 17.5 | 6.3 | | | | 1746 |
| *Mentha arvensis* L. (Field Mint) | | | | | | | | | | | |
| 1 | Leaf | TLC | 61.7 | 7.0 | 16.0 | *)"[? | | tpr=0pt] >15.2 | | | 0 |
| | 1.59[c] | | | | | | | | | | |
| | | 1470 | | | | | | | | | |
| 1 | Stem | TLC | 68.8 | 2.2 | 26.1 | 0 | | | 2.9 | 0.63[c] | 1470 |
| *Mesembryanthemum crystallinum* L. (Ice Plant) | | | | | | | | | | | |
| 1 | Leaf, tonoplast | TLC | 54.4 | 25.4 | 9.7 | | 8.0 | 2.5 | | | 1749 |
| *Metrosideros excelsus* Sol. ex Gaertn. (New Zealand Christmas Tree) | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.25 | | | | | | 1402 |
| *Mnium cuspidatum* Hedw. | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| 1 | –, gametophore | TLC | 58 | 12 | 19 | 12 | | | | 26[a] | 1754 |
| *Mnium marginatum* (With.) Brid. (Olivegreen Calcareous Moss) | | | | | | | | | | | |
| 1 | Whole plant *Incl. LPE | TLC | 28.4 | 22.4 | 30.2 | 11.1* | 7.9 | | | 1.36[c] | 1473 |
| *Mnium medium* Bry. Eur. | | | | | | | | | | | |
| 1 | Gametophore | TLC | 64 | 10 | 15 | 10 | | | | 39[a] | 1754 |
| *Mnium undulatum* Strasb. | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Mucuna pruriens* (L.) DC (Cowitch Bean) | | | | | | | | | | | |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Seed | CC (alumina) | 12.5 | | | | | | | 1806 |
| *Mucuna sloanei* Fawc. and Rend. (Ukpo) | | | | | | | | | | |
| 1 | Seed | TLC | 21 | 25 | 18 | 24 | | | 12 | 2.33[c] 1524 |
| *Muntingia calabura* L. (Calabur) | | | | | | | | | | |
| 1 | Seed | TLC | 19.3 | 21.6 | 3.5 | 30.8 | | | 21.8 | 0.18 1681 |
| *Murraya koenigii* (L.) K. Spreng. (Curry-Leaf) | | | | | | | | | | |
| 1 | Seed | TLC | 28.2 also LPC, 11.1, LPE 14.0 | 32.1 | 5.0 | 7.1 | | 3.0 | | 0.42[c] 1807 |
| *Musa* × *paradisiaca* L. (Banana) | | | | | | | | | | |
| 1 | Shoot tip, micropropagated[cc] | | + | + | + | + | | + | | 1808 |
| *Myrica rubra* Sieb. and Zucc. (Bayberry) | | | | | | | | | | |
| 3 | Seed | TLC | 51.9-55.4 | 10.1-12.8 | | 1.8-4.7 | 32.0-33.0 | | | 0.14-0.45[c] 1809 |
| 3 | –, endocarp | TLC | 49.0-50.0 | 11.9-15.9 | | 1.1-4.5 | 30.4-33.2 | (LPC 0.5-0.9) | | 0.037-0.063[c] 1809 |
| *Myriophyllum quitense* HBK (Water Milfoil) | | | | | | | | | | |
| 1 | Leaf, submerged | TLC | 21.1 | 37.5 | 15.6 | 12.5 | | | | 0.12 1810 |
| 1 | –, aerial | TLC | 26.6 | 32.8 | 19.3 | 13.5 | | | | 0.33 1810 |
| 1 | Stem | TLC | 18.3 | 47.2 | 19.8 | 8.8 | | | | 0.13 1810 |
| 1 | Flower | TLC | 34.5 | 37.2 | 4.4 | 19.5 | | | | 0.24 1810 |
| 1 | Fruit | TLC | 25.8 | 35.2 | | 28.1 | | | | 0.54 1810 |
| 1 | Root | TLC | 21.9 | 34.1 | | 24.3 | | | | 0.27 1810 |
| *Myriophyllum spicatum* L. (Eurasian Water Milfoil) | | | | | | | | | | |
| 1 | Whole plant | TLC | 39.3 | 14.1 | 27.2 | 5.0 | 7.3 | 0.6 | 6.5 | 5.60[c] 1555 |
| *Myriophyllum verticillatum* L. (Myriad Leaf) | | | | | | | | | | |
| 1 | Whole plant | TLC | 38.0 | 16.7 | 15.7 | 18.8 | 4.5 | 6.3 | | 4.40[c] 1445 |
| *Narcissus* spp. (Daffodil) | | | | | | | | | | |
| 1 | Leaf | TLC | | | 11 | | | | | 1440 |
| 1 | Bulb | TLC | + | + | + | + | | | + | 1811 |
| *Nasturtium officinale* R.Br. (Watercress) | | | | | | | | | | |
| 1 | Leaf | TLC | 45.6 | 30.1 | 7.9 | 16.3 | | | | 0.130 1812 |
| *Nelumbo nucifera* Gaertn. (Sacred Lotus) | | | | | | | | | | |
| 1 | Leaf | TLC | 17.2 | 6.9 | 60.4 | 9.7 | | | 5.8 | 3.07[c] 1813 |
| *Nerium oleander* L. (Oleander) | | | | | | | | | | |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Leaf, thylakoid | TLC | 23 | 23 | 45 | 9 | | | | 0.047 | 1814 |
| *Nicotiana glutinosa* L. | | | | | | | | | | | |
| 1 | Leaf chloroplast | TLC | + | + | | | + | | + | | 1815 |
| *Nicotiana quadrivalvis* Pursh (Nonchaw) | | | | | | | | | | | |
| 1 | Leaf | PC | + also LPC + | + | | + | + | | | | 1816 |
| *Nicotiana rustica* L. (Aztec Tobacco) | | | | | | | | | | | |
| 1 | Leaf | TLC | 38.2 | 13.6 | 27.9 | | | | | | 1817 |
| 1 | Callus | TLC | 49.7 | 26.0 | 5.3 | | | | | | 1817 |
| *Nicotiana sylvestris* Speg. and Comes (Woodland Tobacco) | | | | | | | | | | | |
| 1 | Pollen | TLC | 50 | 23 | 2 | 19 | | | 5 | 2.5[c] | 1818 |
| *Nicotiana tabacum* L. (Tobacco) | | | | | | | | | | | |
| 1 | Leaf | TLC | 42 | 12 | 25 | 8 | 8 | | 4 | 0.092 | 1819 |
| 2 | Leaf | TLC | 22.0-34.0 | 11.4-14.3 | 29.5-30.3 | | | | | | 1817 |
| 1 | Leaf[a] | HPLC | 6.3 | 3.5 | 3.7 | 0.9 | 0 | 2.3 | 1.6 | | 1413 |
| 1 | Leaf | PC | 46 | | 28 | 26 | | | | | 1746 |
| 2 | Leaf, air-cured | TLC | 10.3-11.2 | 14.5-15.1 | 6.8-7.0 | 16.0-19.8 | | 13.9-14.8 | 7.3-8.3 | 0.31-0.43[c] | 1820 |
| 2 | Callus | TLC | 42.5-53.9 | 20.2-24.8 | 11.0-41.1 | | | | | | 1817 |
| 1 | Flower, petal | TLC | 46 | 15 | 6 | 21 | 11 | | 1 | 0.157 | 1819 |
| 1 | –, ovary | TLC | 37 | 15 | 6 | 27 | 13 | | 1 | 0.171 | 1819 |
| 1 | –, pistil | TLC | 28 | 10 | 8 | 37 | 14 | | 1 | 0.176 | 1819 |
| 1 | –, anther | TLC | 47 | 18 | 5 | 16 | 12 | | 1 | 0.110 | 1819 |
| 1 | Cell, culture | TLC | 42.5 | 27.0 | 3.8 | 8.4 | | 2.0 | | 0.49[e] | 1495 |
| *Nigella sativa* L. (Black Cumin) | | | | | | | | | | | |
| 1 | Seed | TLC | 32.8 | 28.5 | 6.1 | 25.4 | | | 7.2 | 2.00[c] | 1429 |
| 1 | Seed[n] | HPLC | 0.007 | 0.118 | | 0.0003 | | | | | 1821 |
| *Nitraria komarovii* Iljin and Lava | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 0.3 | 794 |
| *Nitraria schoberi* L. | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 0.7 | 794 |
| *Nothofagus dombeyi* (Mirb.) Oerst. (Coigue) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | 9 | 81 | 6 | | | | 3.2[i] | 1822 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, thylakoid | TLC | 8 | 19 | 52 | 21 | | | | | 1823 |
| 1 | –, envelope membrane | TLC | 15 | 12 | 60 | 13 | | | | | 1823 |
| *Nuphar luteum* (L.) Smith (Yellow Water Lily) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 37.6 | 20.6 | 12.2 | 12.6 | 3.7 | 6.3 | 7.1 | 1.31[c] | 1445 |
| *Nymphoides alba* L. | | | | | | | | | | | |
| 1 | Whole plant | TLC | 46.6 | 25.1 | 11.2 | 9.6 | 2.3 | | 5.3 | 9.20[c] | 1555 |
| *Ocimum basilicum* L. (Basil) | | | | | | | | | | | |
| 1 | Tissue | TLC | + | | | | | | | | 1824 |
| *Oenothera biennis* L. (Evening Primrose) | | | | | | | | | | | |
| 1 | Seed, mature | TLC | 31.9 | 17.6 | 16.7 | 27.1 | | 6.7 | | 0.047[c] | 1825 |
| 1 | –, immature | TLC | 54 | 22 | 4 | 17 | | | | | 1826 |
| *Olea europaea* L. (Olive) | | | | | | | | | | | |
| 1 | Seed | TLC | 48.4 | 6.0 | | 29.3 | | 16.3 | (LPC +) | 0.02 | 1827 |
| 1 | Exocarp | TLC | + | | | + | | | | | 1828 |
| 1 | –, germinated 24 h | TLC | 60.2 | 19.5 | | 10.6 | | 9.7 | | 3781[b] | 1829 |
| 1 | Leaf chloroplast[a] | TLC | 6.1 | | 6.1 | 3.2 | | | | | 1830 |
| 1 | Fruit, kernel | TLC | 47.3 | 7.5 | | 23.9 | Trace | | | 0.41 | 1831 |
| 1 | –, flesh | TLC | 49.3 | 5.3 | | 18.0 | 7.2 | | | 0.36 | 1831 |
| 1 | Fruit, microsomes | TLC | 50.8 | 33.8 | | 4.5 | | 8.4 | | | 1832 |
| 1 | Pollen | TLC | 76.6 | 13.5 | | 5.8 | | 4.0 | | 5266[b] | 1829 |
| 1 | Callus culture | TLC | 42 | 29 | 0 | | | 16 | | 0.093 | 1833 |
| *Oncidium sphacelatum* Lindl. (Golden Shower) | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.42 | | | | | | 1402 |
| *Onopordon acanthium* L. (Scotch Thistle) | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 0.8 | 794 |
| *Onopordon olgae* Bunge and Schmalh. | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 0.2 | 794 |
| *Ophioglossum vulgatum* L. (Southern Adderstongue) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Oreodoxa regia* HBK (Cuban Royal Palm) | | | | | | | | | | | |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]µmol PL/mg protein; [i]µmol PL/mg chlorophyll; [j]µg PL/mg protein; [k]µg lipid P/g; [l]µmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]µmol PL/g dwb; [p]µg PL/100 mg fwb; [q]µg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]µmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]µg PL/mL; [x]µg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]µg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]µg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Seed | TLC | 27.1 | 16.5 | | | | | (LPC 25.1) | | 1799 |
| *Origanum dictamnus* L. (Dittany) | | | | | | | | | | | |
| 1 | Leaf | TLC | 35.5 | 14.4 | 23.3 | 9.0 | 17.8 | | | 1.00 | 1834 |
| *Orobanche crenata* Forsskal. (Broomrape) | | | | | | | | | | | |
| 1 | Whole plant? | TLC | + | + | 0 | + | + | 0 | | | 1835 |
| *Oryza sativa* L. (Rice) | | | | | | | | | | | |
| 1 | Grain, glutinous | TLC | 49.2 | 21.6 | 11.2 | 4.3 | | 4.9 | 9.8 | 0.159 | 1446 |
| 1 | –, endosperm | TLC | 19.3 | 10.1 | | | | (LPC 24.8, LPE 6.4) | | 10.9[a] | 1836 |
| 1 | Grain, nonglutinous, raw | TLC | 28.3 | 11.0 | + | 4.6 | Trace | Trace | | 1.41 | 1837 |
| 1 | –, polished | TLC | 24.0 | 9.2 | + | 3.2 | | | | 0.65 | 1837 |
| 1 | –, polished | Frac. pptn. | | | | | | (LPC 0.2) | | | 1378 |
| 1 | –, bran | TLC | 38.3 | 14.3 | + | 10.9 | TRACE | TRACE | | 5.16 | 1837 |
| 1 | –, endosperm | TLC | 6.0 | 3.0 | | | | (LPC 39.2, LPE 27.0) | 53.3[a] | | 1836 |
| 1 | –, brown | $^{13}$C NMR | | | | | | (LPC +, LPE +) | | | 1838 |
| 1 | –, starch | TLC | | | | | | | (LPC 30.0, LPE 6.9) | 0.29 | 1839 |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 0.7 | 794 |
| 1 | Coleoptile, 7 days old | TLC | 50 | 26 | 5 | 7 | 3 | 6 | 1 | | 1840 |
| 8 | Leaf | TLC | + | | | + | + | | ($Me_2$N-PE trace) | | 1841 |
| 1 | Leaf | TLC | 35 | 19 | 35 | 10 | | | | | 1842 |
| 1 | Anther wall | TLC | 41 | 25 | 26 | 23 | | | | | 1842 |
| 1 | Pollen grain | TLC | 36 | 42 | <0.5 | 22 | | | | | 1842 |
| 3 | Bran | TLC | 35.0-38.4 | 27.2-29.0 | 1.4-1.8 | 21.0-23.3 | | 7.2-9.6 | | 0.98-1.12 | 1843 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | also NAPE 0.7-0.8, LPC 1.0-1.5, LPE 1.0-1.4 | | | | | | | | |
| 2 | Bran (1) | TLC | 14.2 | 34.2 | 8.9 | 9.0 | 7.3 | | (LPC 1.6) | 8.1 | 1844 |
| | Bran (2) | | 10.2 | 40.5 | 10.3 | 13.5 | 5.3 | | (LPC 1.6) | 3.5[a] | |
| 1 | Bran, glutinous | TLC | + | + | + | + | + | | | (NAPE +, LPC +, LPE +) | 1845 |
| 1 | –, nonglutinous | TLC | + | + | + | + | + | | (NAPE +, LPC +, LPE +) | | 1845 |
| 1 | Bran, spherosomes | TLC | 63.8 | 7.2 | 1.4 | Trace | 1.8 | 2.7 | 1.8 | 0.9[c] | 1846 |
| | | | also NAPE 5.4, NALPE 5.0, LPC 9.5, and LPE 1.4 | | | | | | | | |
| 2 | *)"[?tpr=0pt] >Starch (1) | TLC | 9.5 | 2.2 | | | | (LPC 58.2, LPE 30.0) | 42.7 | | 1847 |
| | Starch (2) | TLC | | | | | (LPC 81.3, LPE 18.7) | | | 57.7 | |
| 2 | Protein bodies (1) | TLC | 10.7 | 10.0 | | | (LPC 45.7, LPE 33.6) | | | 14.0 | 1847 |
| | Protein bodies (2) | TLC | 14.1 | 6.3 | | | (LPC 44.4, LPE 35.2) | | | 14.2 | |
| 1 | Shoot, plasma membrane | HPLC | 39 | 31 | | 10 | 20 | | | 0.034[k] | 1848 |
| 4 | Seedling mitochondria | TLC | 48.5-51.4 | 20.2-21.5 | 3.5-5.5 | 5.9-6.8 | 1.1-2.0 | 8.8-10.4 | 3.4-4.6 | (LPC 1.3-3.3) | 1849 |
| 1 | Cell suspension culture | TLC | | | | | (NAPE +) | | | | 1361 |
| 2 | Cell culture, tonoplast | TLC | 45.4-50.5 | 32.9-36.0 | 5.2-6.1 | 7.8-9.3 (incl. PS) | | 2.7-4.2 | | | 1850 |
| 2 | –, plasma membrane | TLC | 37.8-40.5 | 40.5-41.3 | 7.3-7.8 | 7.6-9.2 (incl. PS) | | 3.6-4.5 | | | 1850 |
| *Paeonia decora* Anders. (Peony) | | | | | | | | | | | |
| 1 | Seed[cc] | | + | + | | | | | | | 1851 |
| *Palisota barteri* Hook.f. | | | | | | | | | | | |
| 1 | Berry, chromoplast | | TLC | + | + | + | + | | | | 1852 |
| *Panax ginseng* C.A. Meyer (Ginseng) | | | | | | | | | | | |
| 1 | Root | TLC | 25.0 | 26.8 | 28.8 | 12.0 | | 1.6 | | 0.202 | 1853 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]µmol PL/mg protein; [i]µmol PL/mg chlorophyll; [j]µg PL/mg protein; [k]µg lipid P/g; [l]µmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]µmol PL/g dwb; [p]µg PL/100 mg fwb; [q]µg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]µmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]µg PL/mL; [x]µg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]µg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]µg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, periderm | TLC | 24.8 | 9.8 | 11.0 | 7.3 | | 17.2 | | 0.232 | 1853 |
| 1 | –, cortex | TLC | 28.5 | 21.6 | 32.2 | 8.1 | | 2.5 | | 0.145 | 1853 |
| 1 | –, medulla | TLC | 38.2 | 15.4 | 33.7 | 5.2 | | 1.0 | | 0.207 | 1853 |
| *Panicum dichotomiflorum* Michx. (Fall Panicum) | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.62 | | | | | | 1402 |
| *Panicum miliaceum* L. (Proso Millet) | | | | | | | | | | | |
| 1 | Seed | TLC | 27.5 | 20.1 | | 22.3 | 14.0 | 13.3 | (LPC 2.8) | 0.41 | 1854 |
| 9 | Seed, flour | TLC | + | + | | | + | | | 0.47-0.89 | 1855 |
| 9 | –, bran | TLC | + | + | | | + | | | 0.30-0.70 | 1855 |
| *Panicum sumatrense* Roth (Little Millet) | | | | | | | | | | | |
| 1 | Grain | TLC | 36.5 | 21.0 | 8.0 | Trace | Trace | 5.5 | (LPC 28.0) | 0.41[c] | 1662 |
| *Papaver dubium* L. (Field Poppy) | | | | | | | | | | | |
| 1 | Pollen | TLC | 54.7 | 25.4 | 2.6 | 11.4 (incl. PS) | | 1.5 | 4.5 | | 1856 |
| *Papaver somniferum* L. (Opium Poppy) | | | | | | | | | | | |
| 4 | Fruit juice | PC | 16.4-70.0 | 30.0-83.6 | | | | | | | 1857 |
| *Parkinsonia aculeata* L. (Mexican Palo Verde) | | | | | | | | | | | |
| 1 | Seed | TLC | 23.3 | 22.3 | | | 29.1 | | (LPC 25.2) | 3.5 | 1858 |
| *Parthenocissus tricuspidata* (Sieb. and Zucc.) Planch. (Boston Ivy) | | | | | | | | | | | |
| 1 | Cell culture, callus | TLC | 53 | 37 | | 8 | | 1 | | | 1859 |
| 1 | –, protoplast | TLC | 36 | 28 | | 9 | | 27 | | | 1859 |
| *Paspalum dilatatum* Poir. (Dallis Grass) | | | | | | | | | | | |
| 1 | Leaf | TLC | 28 | 13 | 35 | 7 | | (LPC 10) | 7 | 1.38[l] | 1523 |
| *Paspalum distichum* L. (Knotgrass) | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.61 | | | | | | 1402 |
| *Paspalum scrobiculatum* L. (Kodo Millet) | | | | | | | | | | | |
| 1 | Grain | TLC | 21.2 | 30.2 | 18.0 | Trace | Trace | 9.0 | (LPC 20.1) | 0.20[c] | 1662 |
| *Pastinaca hirsuta* L. | | | | | | | | | | | |
| 1 | Seed | TLC | 36 | 9 | 5 | 31 | | 11 | 1 | 1.7[a] | 1438 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | also LPC 5 | | | | | | | | |
| *Pastinaca sativa* L. (Parsnip) | | | | | | | | | | | |
| 1 | Root | TLC | 38 | 20 | 8 | 12 | | | 22 | 0.88[l] | 1523 |
| *Peganum harmala* L. (African Rue) | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 0.2 | 794 |
| *Pellia neesiana* (Gott.) Limpr. (Ring Pellia) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 30.1 | 15.7 | 23.0 | 5.8 | 18.5 | | | 2.98[c] | 1551 |
| *Pennisetum glaucum* (L.) R.Br. (Pearl Millet) | | | | | | | | | | | |
| 1 | Seed | TLC | 24.3 | 6.4 | 1.1 | Trace | Trace | 1.2 | | 7.19[c] | 1860 |
| | | | also LPC 41.6, LPE 21.2 | | | | | | | | |
| 1 | Pollen grain | TLC | 55.1 | 31.3 | 1.3 | 7.6 (incl. PS) | | 3.2 | 1.3 | 4.99[c] | 1861 |
| *Penstemon speciosus* Dougl. | | | | | | | | | | | |
| 1 | Pollen | TLC | | + | + | + | | | | | 1603 |
| *Pentaclethra macrophylla* Bentl. (African Oil Bean) | | | | | | | | | | | |
| 1 | Seed | TLC | 27 | 18 | 22 | 22 | | | 11 | 1.72[c] | 1524 |
| *Perilla frutescens* (L.) Britt. (Perilla Mint) | | | | | | | | | | | |
| 2 | Seed | TLC | 25- | 18 | 20-25 | 5-17 | | | (LPC 10- | 4.0-4.5[a] | 1862 |
| | *Incl.PS | | 46* | | | | | | 14) | | |
| 5 | Seed | TLC | 17.6- | 50.4-57.1 | | 4.8-6.6 (incl. PS) | | 13.6- | | 2.0-3.0[c] | 1863 |
| | | | 20.6 | | | | | 19.9 | | | |
| 2 | Seed | TLC | + | + | | + | | | | | 1864 |
| *Persea americana* Mill. (Avocado) | | | | | | | | | | | |
| 1 | Fruit, kernel | TLC | 44.9 | 15.0 | | 12.1 | | | | 4.2 | 1831 |
| 2 | –, flesh (1) | TLC | 37.0 | 19.5 | | 18.0 | | | | 1.63 | 1831 |
| | –, flesh (2) | TLC | 38.5 | 12.0 | | 16.5 | | | | 1.43 | 1831 |
| 1 | Fruit, mitochondria | TLC | 45 | 21 | 5 | 11 | 4 | 5 | 9 | | 1865 |
| 1 | –, chloroplast | TLC | 34 | 33 | 6 | 12 | 6 | | 9 | | 1865 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]µmol PL/mg protein; [i]µmol PL/mg chlorophyll; [j]µg PL/mg protein; [k]µg lipid P/g; [l]µmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]µmol PL/g dwb; [p]µg PL/100 mg fwb; [q]µg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]µmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]µg PL/mL; [x]µg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]µg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]µg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Petroselinum crispum* (Mill.) Nym. (Parsley) | | | | | | | | | | | |
| 1 | Leaf[a] | TLC | 15.5 | 5.9 | 5.4 | | | | | 0.18 | 1866 |
| 1 | Root[a] | TLC | 9.3 | 6.2 | 10.8 | 7.7 | | | | 0.28 | 1866 |
| 1 | Cell culture[a] | TLC | 32.9 | 18.0 | 3.1 | Trace | | | | 0.08 | 1866 |
| 1 | Fruit (also LPC 1.9, LPE 2.9) | TLC | 38.5 | 16.5 | 0.9 | 32.0 | | 4.4 | | 0.5 | 1471 |
| *Petunia hybrida* hort. (Petunia) | | | | | | | | | | | |
| 1 | Cell culture, callus | TLC | 14 | 6 | | 4 | | 1 | 0.5 | | 1859 |
| 1 | –, protoplast | TLC | 41 | 15 | | 20 | | 24 | | | 1859 |
| *Pharbitis nil* Choisy (Morning Glory) | | | | | | | | | | | |
| 1 | Leaf | TLC | 44 | 17 | 27 | 10 | | 2 | | 37.0[s] | 1867 |
| *Phaseolus coccineus* L. (Scarlet Runner Bean) | | | | | | | | | | | |
| 1 | Bean | TLC | 40.9 | 23.5 | 3.5 | 20.4 | (NAPE 9.6) | | | 1.24 | 1693 |
| 1 | Leaf | CC (silica) | 31 | 20 (incl. PS) | | 45 | | | | | 1356 |
| 1 | Leaf[a] | TLC | 12.3 | 12.5 | | 3.6 | | | | | 1868 |
| 1 | –, chloroplast[g] | TLC | 3.5 | | 5.1 | | | | | | 1869 |
| 1 | –, PS(II) particle[m] | TLC | 0.023 | | 0.042 | | | | | | 1870 |
| *Phaseolus lunatus* L. (Lima Bean) | | | | | | | | | | | |
| 1 | Seed[c] | Frac. pptn. | 0.622 | 0.089 | | | | | | | 718 |
| 1 | Bean | TLC | 43.7 | 47.4 | | 8.9 | | | | 1.391 | 1446 |
| 1 | Root tip plasmalemma | TLC | + | + | ? | + | | (LPC ?) | | | 1871 |
| *Phaseolus vulgaris* L. (Bean (common)) | | | | | | | | | | | |
| 3 | Seed | TLC | 30.2-36.2 | 30.6-53.6 | | 7.0-15.1 | 5.6-22.8 | | | 0.75-0.98 | 1872 |
| 4 | Whole bean | TLC | 28.9-68.6 | 8.9-32.8 | | 3.4-17.5 | | 0.01-18.0 | | 0.28-1.11[c] | 1873 |
| 1 | Seed | TLC | 21 | 28 | 28 | 13 | | | 9 | 0.26[c] | 1524 |
| 1 | –, cotyledon vesicle | TLC | 60 | 21 | | 19 | | | | 0.41[h] | 1874 |
| 1 | –, hypocotyl mitochondria | TLC | 30.4 | 24.0 | 15.7* | 9.9[¶] | *iNcl. DPG | [¶]Incl. PS | | (LPC 2.4) | 1875 |
| 1 | Seed | TLC | 37.5 | 25.7 | | 20.4 | | 0.5 | | 2.0 | 1876 |
| | | | also NAPE 7.7, NALPE 3.4, LPC 3.4 | | | | | | | | |
| 1 | Seed, cotyledon | $^{31}$P NMR | + | + | | + | | (LPC +) | | | 49 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, embryonic axis | $^{31}$P NMR | + | + | | | | | | 49 |
| 1 | Starch | TLC | | | | | | (LPC 5.1, LPE 2.0) | 0.15 | 1499 |
| 1 | Leaf | TLC | 38.9 | 27.0 | 23.7 | 10.4 | Trace | | 1733[r] | 1634 |
| 1 | Leaf | TLC | 44 | 19 | 28 | 7 | | 2 | 71.1[s] | 1867 |
| 1 | Leaf | PC | 41 | 19 | 30 | 11 | | | | 1517 |
| 6 | Leaf | TLC | 34.2-45.0 | 16.0-20.5 | 23.5-29.5 | 5.5-9.0 | 2.2-3.7 | 1.7-2.7 | 1.2-5.0 | 1877 |
| 1 | Leaf, chloroplast | TLC | | | 12[a] | | | | | 1489 |
| 1 | Leaf, thylakoid membrane | TLC | 29.4 | | 67.2 | | | | 81[n] | 1878 |
| 1 | Leaf, 2 weeks | TLC | 41.1 | 8.5 | 33.5 | 6.7 | | | 2.24[c] | 1879 |
| 1 | Root, 2 weeks | TLC | 32.0 | 9.0 | 38.5 | 6.4 | | | 0.78[c] | 1879 |
| 1 | Root[l] | Choline | 1 | | | | | | | 1451 |
| 1 | Root, mitochondria – ssp. *humilis* | TLC Bush Bean | 47.3 | 38.4 | 4.0 | | | 10.3 | | 1880 |
| 1 | Bean[bb] | Choline | 1 | | | | | | | 1451 |
| *Philonotis fontana* (Hedw.) Brid. | | | | | | | | | | |
| 1 | Whole plant | TLC | 12.3 | 35.9 | 28.9 | 9.4 | 13.5 | | 0.62[c] | 1493 |
| *Phoenix dactylifera* L. (Date Palm) | | | | | | | | | | |
| 3 | Seed | TLC | 20.5-22.5 | | | | | (LPC 19.5-22.0) | | 1799 |
| *Phoenix sylvestris* (L.) Roxb. (Wild Date Palm, Kharjur) | | | | | | | | | | |
| 1 | Seed | TLC | 38.7 also LPC 0.4, LPE 0.3 | 20.7 | | 27.2 | | 12.7 | 0.45[c] | 1757 |
| *Phragmites communis* Trin. (Water Reed) | | | | | | | | | | |
| 4 | Plasmalemma | TLC | | | | | | 4.3-18.8 | | 1881 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 5.4-12.8 | 5.4-14.0 | 24.3-61.1 | 6.1-20.7 | | 11.3-28.0 | | | |
| *Phyllitis scolopendrium* L. (Hart's Tonguefern) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Phyllospadix iwatensis* Makino | | | | | | | | | | | |
| 1 | Whole plant (NAPE tr) | TLC | 42.7 | 22.4 | 16.6 | 13.7 | 1.5 | Trace | 3.3 | 0.14 | 1882 |
| *Phyllostachys pubescens* Mazel (Moso Bamboo) | | | | | | | | | | | |
| 1 | Shoot, peeled | TLC | 49.4 and variation from tip to base of shoot | 21.6 | 11.0 | 8.7 | 5.5 | (LPC tr.) | 3.7 | 0.044[k] | 1883 |
| *Picea abies* (L.) Karst. (Norway Spruce) | | | | | | | | | | | |
| 1 | Needles (leaf) | TLC | 48.1 | 8.4 | 33.2 | 10.2 | | | | 1.21[i] | 1884 |
| 1 | –, thylakoid | TLC | 45.8 | 8.0 | 32.3 | 13.9 | | | | 0.85[i] | 1884 |
| 1 | –, envelope | TLC | 32.7 | 9.2 | 42.1 | 16.0 | | | | 0.067[i] | 1884 |
| 1 | –, chloroplast[q] | TLC | | | 433 | | | | | | 1885 |
| *Picea mariana* (Mill.) BSP (Black Spruce) | | | | | | | | | | | |
| 1 | Shoot | TLC | 37 | 20 | 31 | 12 | | | | 0.61[c] | 1886 |
| *Pimpinella acuminata* (Edgew.) C. B. Clarke | | | | | | | | | | | |
| 1 | Seed[a] | TLC | 1.2 | 0.8 | | 1.2 | (LPC 0.4) | | | 30.0 | 1887 |
| *Pimpinella anisum* L. (Anise) | | | | | | | | | | | |
| 1 | Fruit | TLC | 51.1 also LPC 3.6, LPE 4.1 | 11.1 | 1.9 | 20.4 | | 4.4 | | 0.3 | 1471 |
| *Pinus armandii* Franch. (Armand Pine) | | | | | | | | | | | |
| 1 | Seed | TLC | 44.9 | 22.3 | | | 12.3 | | | 0.38 | 1888 |
| *Pinus banksiana* Lamb. (Jack Pine) | | | | | | | | | | | |
| 1 | Seedling | TLC | 31.3 | | 54.8 (incl. PG) | 13.9 | | | | 0.073 | 1889 |
| *Pinus cembra* L. (Swiss Stone Pine) | | | | | | | | | | | |
| 1 | Kernel[n] | TLC | 5.4 | 1.1 | | 3.0 | 0 | | (Phyto-GP 0.4) | | 1481 |
| *Pinus halepensis* Mill. (Aleppo Pine) | | | | | | | | | | | |
| 1 | | TLC | 34.7 | 22.2* | 10.2 | 11.0 | | 12.6 | 9.1 | | 1699 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Root | | | | | | | | | |
| | *Incl. PS | | | | | | | | | |
| 1 | Pollen | TLC | 44.4 | 26.5 | | 27.3 | | | 1.05[c] | 1890 |
| | | | also LPC 1.5, LPE 0.3 | | | | | | | |
| 1 | Pollen | HPLC | 40.1 | 25.0 | 0 | 22.8 | 0 | 0 | 1.01 | 1890 |
| *Pinus koraiensis* Sieb. and Zucc. (Korean Pine) | | | | | | | | | | |
| 1 | Nut | TLC | 40.2 | 19.4 | | 7.3 | 2.6 | (LPC 5.3) | 0.6 | 1891 |
| *Pinus mugo* Turra (Mugo Pine) | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | | | | | | 1436 |
| *Pinus nigra* Arnold (Black Pine) | | | | | | | | | | |
| 1 | Needle | HPLC | 42 | 20 | 23 | | | | 0.30 | 1892 |
| *Pinus pinaster* Ait. (Cluster Pine) | | | | | | | | | | |
| 1 | Root | TLC | 39.9 | 24.2* | 6.0 | 14.0 | 7.3 | 8.5 | | 1699 |
| | *Incl. PS | | | | | | | | | |
| *Pinus pinea* L. (Italian Stone Pine) | | | | | | | | | | |
| 1 | Seed, germ, 7 days | TLC | 38.1 | 15.2 | 2.9 | 17.9 | 4.2 | 11.3 | | 1893 |
| 1 | Root | TLC | 33.2 | 34.6* | 10.3 | 8.2 | 4.6 | 9.1 | | 1699 |
| | *Incl. PS | | | | | | | | | |
| *Pinus ponderosa* Dougl. (Ponderosa Pine) | | | | | | | | | | |
| 1 | Pollen | TLC | 60 | 18 | 6 | 13 | 1 | 2 | 2.9[c] | 1894 |
| *Pinus radiata* D. Don (Monterey Pine) | | | | | | | | | | |
| 1 | Leaf | TLC | 35 | 12 | 24 | 16 | | 13 | 2.30[l] | 1523 |
| 1 | Root | TLC | 29.5 | 24.0 | 13.8 | 13.8 | 11.1 | 7.7 | | 1699 |
| | *Incl. PS | | | | | | | | | |
| *Pinus sibirica* Du Tour (Siberian Stone Pine) | | | | | | | | | | |
| 1 | Seed, germ | TLC | 20.8 | 17.7 | | 14.8 | 11.6 | 17.3 | (LPC 10.2) | 8.1 | 1895 |
| 1 | –, endosperm | TLC | 19.3 | 17.7 | | 12.8 | 11.1 | 21.4 | (LPC 8.9) | 1.7 | 1895 |
| *Pinus sylvestris* L. (Scotch Pine, Scots Pine (Brit.)) | | | | | | | | | | |
| 1 | Needle | TLC | + | + | + | + | | + | + | | 1896 |
| 1 | Needle (leaf) | TLC | | 6.5 | 41.8 | 21.9** | | 29.8 | | 2.17[l] | 1897 |
| | *Incl. PC,PS | | | | | | | | | |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]µmol PL/mg protein; [i]µmol PL/mg chlorophyll; [j]µg PL/mg protein; [k]µg lipid P/g; [l]µmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]µmol PL/g dwb; [p]µg PL/100 mg fwb; [q]µg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]µmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]µg PL/mL; [x]µg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]µg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]µg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, thylakoid | TLC | | 3.9 | 35.2 | 30.5* | | 30.9 | | | 1897 |
| 1 | –, chloroplast | TLC | 27.3 | 0 | 25.4 | 23.7 | 23.5 | | | 0.068 | 1797 |
| 1 | Seedling[l] | TLC | 2.38 | 1.01 | 1.10 | 0.55 (incl. PS) | | | | | 1898 |
| 1 | Wood<br>*Incl. PG | TLC | 62.1 | 14.6* | | 5.8 | | 1.0 | 14.0 | 1.71[a] | 1899 |
| *Pistacia vera* L. (Pistachio) | | | | | | | | | | | |
| 1 | Nut | TLC | 63<br>also LPC 5.6 | 22 | | + | + | 7 | 7 | 1.07 | 1900 |
| *Pistia stratiotes* L. (Water Lettuce) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 46.2 | 26.2 | 6.0 | 8.6 | 7.7 | Trace | 5.0 | 2.87[c] | 1555 |
| *Pisum sativum* L. (Peas) | | | | | | | | | | | |
| 3 | Whole pea | TLC | 54.3 | 16.1 | | 17.1 | | | | | 1901 |
| 3 | –, cotyledon | TLC | 52.9 | 14.5 | | 14.1 | | | | | 1901 |
| 1 | –, mitochondria | TLC | 52.2<br>also LPC 6.7 LPE 3.8 | 15.5 | | 13.6 | | | 5.1 | | 1901 |
| 3 | Cotyledon, starch | TLC | 0 | + | | | + | | (LPC 0, LPE +, LPS +) | | 1902 |
| 1 | Seed | PC | | | | (NAPE +, NALPE +) | | | | | 1498 |
| 1 | Seed | TLC | 41.6<br>also LPC 7.8 | 15.5 | 6.5 | 2.6 | | 15.6 | 10.4 | 0.38 | 1903 |
| 1 | Seed | TLC | 45.7 | 16.2 | 3.2 | 20.8 | | | (NAPE 12.1) | 1.22 | 1693 |
| 1 | Seed | TLC | +<br>also LPC +, LPE +, NAPE +, and NALPE + | + | + | + | + | + | + | | 1904 |
| 1 | Seed | TLC | 54.6<br>also LPC 2.5, LPE 1.3 | 17.0 | 2.2 | 21.2 | 0.6 | 0.7 | | 1.55[c] | 1905 |
| 1 | –, starch granule | TLC | | | | | | (LPC 0, LPE 0) | | | 1905 |
| 1 | Seed | HPLC | + | + | + | + | + | + | | | 1804 |
| 1 | Seed | TLC | | | | | Alkenyl PC 0.6, PE 0.2 | | | | 1906 |
| 1 | 3-day seedling | TLC | | | | | | Alkenyl PC 1.2-1.8, PE 0.4-0.6 | | | 1906 |
| | | Both plasmalogens are 1-alken-1′-yl-2-acyl PL's where the alkenyl group is mainly 16:0, 18:1, and 18:2 | | | | | | | | | |
| 1 | 24-h seedling, microsomes[a] | TLC | 53.9 | 11.1 | | 15.8 | | | | | 1907 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Stems and petioles | TLC | 40.5 | 27.3 | 12.3 | 16.2 | | 3.7 | | 0.157 | 1638 |
| 1 | Leaf | TLC | | | | | + | | | | 1450 |
| 1 | Leaf[m] | TLC | 0.55 | | 0.37 | | | | | 1.23[m] | 1908 |
| 1 | –, chloroplast | TLC | 22 | 0 | 71 | 7 | | | | | 1909 |
| 1 | –, mitochondria | TLC | 44.7 | 32.1 | 1.9 | 2.7 | | | 18.6 | | 1909 |
| 1 | –, thylakoid[m] | TLC | 0.24 | | 0.32 | | | | | 0.75[m] | 1908 |
| 1 | Shoot, chloroplast membrane | TLC | 77.2 | 2.4 | 12.6 | 6.9 | | | | | 1910 |
| 1 | –, inner (heavy) | TLC | 49.5 | 4.4 | 32.8 | 10.8 | | | | | 1910 |
| 1 | –, outer (light) | TLC | 78.2 | 2.7 | 9.8 | 9.1 | | | | | 1910 |
| 1 | Root, microsomes[j] | HPLC | 0.54 | 0.37 | | 0.04 | | | | | 1911 |
| 1 | –, symbiosomes[j] | HPLC | 0.44 | 0.27 | | 0.01 | | | | | 1911 |
| 1 | –, plasmalemma[j] | HPLC | 0.13 | 0.34 | | 0.00 | | | | | 1911 |
| 1 | Root, plastids[g] | TLC | 47.5 | 9.2 | 16.4 | 1.7 | 1.3 | 7.1 | | (LPC 4.2, LPA 12.6) | 1912 |
| *Plagiomnium ellipticum* (Brid.) T. Kop. | | | | | | | | | | | |
| 1 | Whole plant *Incl. LPE | TLC | 28.6 | 21.0 | 30.6 | 11.4* | 8.4 | | | 0.15[c] | 1473 |
| *Plagiomnium medium* (Bruch et Schimp. in B.S.G.) T. Kop. | | | | | | | | | | | |
| 1 | Whole plant | TLC | 35.3 | 14.0 | 27.3 | 12.2 | 11.4 | | | 0.54[c] | 1493 |
| *Platanus* spp. (Plane Tree) | | | | | | | | | | | |
| 1 | Leaf | TLC | 32.3 | 24.2 | 22.0 | 0 | Trace | | | 223[r] | 1634 |
| *Platycerium alcicorne* (Willem.) Tardieu | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Pleurozium schreberi* (Brid.) Mitt. | | | | | | | | | | | |
| v1 | Whole plant *Incl. LPE | TLC | 55.6 | 20.0 | 15.5 | 8.9* | | | | 0.34[c] | 1654 |
| 1 | –, gametophore | TLC | 67 | 13 | 7 | 13 | | | | 15[a] | 1754 |
| *Poa annua* L. (Annual Bluegrass) | | | | | | | | | | | |
| 1 | Leaf, thylakoid[a] | TLC | | | 9.7 | | | | | | 1913 |
| *Poa pratensis* L. (Kentucky Bluegrass) | | | | | | | | | | | |

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*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Leaf | TLC | 29.6 | 19.6 | 27.1 | 3.7 | 1.9 | 18.1 | Trace | 0.85[x] | 1914 |
| *Podocarpus nivalis* Hook. (Snow Totara) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | | | | | | | 1436 |
| *Podocarpus nubigenus* Lindl. (Cloud Podocarp) | | | | | | | | | | | |
| 1 | Needle | TLC | 36 | 21 | 21 | 21 | | | | l.4[o] | 1915 |
| *Podocarpus salignus* D. Don (Willow Podocarp) | | | | | | | | | | | |
| 1 | Needle | TLC | 5 | 50 | 15 | 30 | | | | 2.0[o] | 1915 |
| *Polygonum amphibium* L. (Water Smartweed) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 46.9 | 15.9 | 13.0 | 12.2 | 1.3 | 10.7 | | 0.89[c] | 1445 |
| *Polypodium vulgare* L. (European Polypody) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Polytrichum commune* Hedw. (Polytrichum Moss) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Polytrichum juniperinum* Hedw. (Hair Cap Moss) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 24.6 | 20.4 | 21.9 | 9.0 | 12.0 | | | 0.42[c] | 1493 |
| *Poncirus trifoliata* L. × *Citrus paradisi* Macf. (Citrumelo) | | | | | | | | | | | |
| 1 | Leaf | TLC | 64.5 | 20.9 | 6.9 | 7.7 | | | | 0.363 | 1590 |
| *Pongamia glabra* Vent. (Pongam, Karanja) | | | | | | | | | | | |
| 1 | Seed, kernel | TLC | 43.1 | 18.8 | | 33.3 | | | | 0.78 | 1916 |
| *Populus euroamericana* (Dode) Guin. (Carolina Poplar) | | | | | | | | | | | |
| v1 | Bark | CC (silica) | 44.3 | 19.3 | 10.7 | 11.4 | | | | 14.0[o] | 1917 |
| *Populus nigra* L. var. *italica* (Lombardy Poplar) | | | | | | | | | | | |
| 1 | Leaf | TLC | 40 | 18 | 24 | 11 | | | 8 | 4.55[l] | 1523 |
| *Portulaca grandiflora* Hook. (Rose Moss) | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.26 | | | | | | 1402 |
| *Portulaca oleracea* L. (Purslane) | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.26 | | | | | | 1402 |
| *Posidonia oceanica* (L.) Delile (Mediterranean Tapeweed) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 41.9 | 23.1 | 17.7 | 12.8 | 1.9 | Trace | 2.9 | 0.53[c] | 1555 |
| *Potamogeton filiformis* Pers. | | | | | | | | | | | |
| 1 | Whole plant | TLC | 25.6 | 15.6 | 28.2 | 5.2 | 5.5 | 2.3 | 17.6 | 18.0 | 1789 |
| *Potamogeton natans* L. (Floating Leaf Pondweed) | | | | | | | | | | | |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Whole plant | TLC | 38.7 | 16.9 | 11.4 | 6.1 | 4.0 | 7.4 | 15.4 | 29.7 | 1789 |
| *Potamogeton perfoliatus* L. (Perfoliate Pondweed) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 41.4 | 11.0 | 24.9 | 9.9 | 4.1 | 8.7 | | 1.97[c] | 1445 |
| *Potentilla asiatica* Juz. (Cinquefoil) | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 0.4 | 794 |
| *Pringlea antiscorbutica* R.Br. (Kerguelen Cabbage) | | | | | | | | | | | |
| 1 | Leaf | TLC | 41.5 | 23.1 | 22.4 | 11.6 | | | 1.4 | 1.47[c] | 1918 |
| *Prunus armeniaca* L. (Apricot) | | | | | | | | | | | |
| 1 | Seed kernel | TLC | 43.0 also LPC 0.8, LPE 0.5 | 15.2 | 1.3 | 31.6 | 1.1 | 3.1 | 0.4 | 0.5 | 1919 |
| 1 | Root *Incl. PS | TLC | 41.6 | 36.0* | 8.8 | 1.1 | | 7.0 | 5.5 | | 1699 |
| *Prunus avium* (L.) L. (Cherry) | | | | | | | | | | | |
| 1 | Seed kernel | TLC | 41.0 also LPC 1.0, LPE 1.0 | 14.7 | 1.0 | 30.0 | 2.7 | 4.7 | 0.8 | 0.4 | 1919 |
| 3 | Seed embryo | TLC | 40.3-43.1 | 36.3-39.4 | | 2.4-2.7 | 12.3-14.4 | | (LPC 1.8-3.1) | 0.34-0.56[c] | 1920 |
| 3 | –, endocarp | TLC | 39.3-40.4 | 39.7-43.9 | | 6.2-7.3 | 3.8-4.7 | | (LPC 3.5-4.3) | 0.30-0.49[c] | 1920 |
| 1 | Leaf[f] | TLC | | | 1.3-2.2 | | | | | | 1921 |
| 1 | Callus culture | TLC | 35 | 17 | 39 | 9 (incl. PS) | | | | | 1922 |
| *Prunus cerasus* L. (Morello Cherry) | | | | | | | | | | | |
| 1 | Seed kernel | TLC | 37.4 also LPC 0.6, LPE 1.7 | 19.5 | 2.8 | 21.5 | 9.7 | 4.3 | 2.8 | 0.4 | 1919 |
| *Prunus domestica* L. (Plum) | | | | | | | | | | | |
| 1 | Seed kernel | TLC | 59.8 also LPC 1.6, LPE 1.9 | 16.0 | 0.4 | 13.8 | 0.0 | 1.2 | 1.5 | 0.2 | 1919 |
| *Prunus dulcis* (Mill.) D.A. Webb (Almond) | | | | | | | | | | | |
| 1 | seed kernel, mature | TLC | 14.3 | 2.1 | 8.0* | 12.2 | 0.9[¶] | 1.6 | 58.8 | | 1923 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]µmol PL/mg protein; [i]µmol PL/mg chlorophyll; [j]µg PL/mg protein; [k]µg lipid P/g; [l]µmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]µmol PL/g dwb; [p]µg PL/100 mg fwb; [q]µg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]µmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]µg PL/mL; [x]µg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]µg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]µg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, immature | TLC | 23.6<br>*Incl. sulfolipids<br>¶Incl. lysolipids | 3.0 | 6.4* | 18.8 | 1.2¶ | 1.6 | 45.2 | | 1923 |
| 1 | Root<br>*Incl. PS | TLC | 38.2 | 33.5* | 9.0 | 3.1 | | 10.1 | | | 1699 |
| *Prunus mume* Sieb. and Zucc. (Ume Apricot) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | + | | | (NAPE +) | 0.245 | 1924 |
| *Prunus persica* (L.) Batsch. (Peach) | | | | | | | | | | | |
| 2 | Whole seed | TLC | 43.7-44.7 | 35.5-37.4 | | | 17.1-19.9 | | | 0.09-0.12 | 1925 |
| 2 | –, endocarp | TLC | 38.5-40.5 | 50.0-50.3 | | 4.5-6.6 | 2.4-6.0 | | | 0.002-0.006 | 1925 |
| 1 | Seed kernel | TLC | 38.2<br>also LPC 5.0, LPE 1.8 | 12.9 | 1.5 | 29.2 | 0.9 | 7.1 | 1.0 | 0.2 | 1919 |
| 1 | Leaf | TLC | 27.0 | | 73.0 | | | | | | 1926 |
| 1 | Root<br>*Incl. PS | TLC | 46.6 | 36.3* | 8.7 | 1.3 | | 4.2 | 2.9 | | 1699 |
| *Pseudobryum cinclidiodes* (Hueb.) T. Kop. | | | | | | | | | | | |
| 1 | Whole plant | TLC | 14.2 | 20.7 | 35.0 | 15.0 | 15.1 | | | 0.27[c] | 1493 |
| *Psilotum triquetrum* Swartz. | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Psophocarpus tetragonolobus* (L.) DC (Winged Bean) | | | | | | | | | | | |
| 1 | Seed | TLC | 37 | 27 | 8 | 18 | 2 | | 7 | 0.73 | 1927 |
| 4 | Bean<br>*Incl. LPE | TLC | 35-43* | 18-22 (incl. PG) | | 16-27 | | (NAPE 1-3) | | 1.18-1.51 | 1928 |
| *Psoralea drupacea* Bunge (Drupe Scurf Pea) | | | | | | | | | | | |
| 1 | Seed | TLC | 35.3<br>Also given: NAPE 7.2, NALPE 3.2, LPC 3.0 | 23.4 | | 21.8 | | | | 1.1[c] | 1929 |
| *Pteridium aquilinum* (L.) Kuhn (Bracken Fern) | | | | | | | | | | | |
| 1 | Pinnae | TLC | 72 | | 9 | 14 | | | 4 | 1.58 | 1930 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Upper rachis | TLC | 61 | | 15 | 15 | | | 10 | 0.61 | 1930 |
| 1 | Petiole, upper | TLC | 56 | | 20 | 12 | | | 12 | 0.25 | 1930 |
| 1 | –, lower | TLC | 86 | | tr | 14 | | | Trace | 0.21 | 1930 |
| 1 | Rhizome, storage | TLC | 58 | | 17 | 8 | | | 17 | 0.12 | 1930 |
| 1 | –, frond-bearing | TLC | 50 | | Trace | Trace | | | 50 | 0.02 | 1930 |
| *Punica granatum* L. (Pomegranate) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | + | | + | (LPC +, LPI +) | 1.0 | 1931 |
| 1 | Seed | TLC | + | | | + | + | | | 2.9 | 1932 |
| *Pyrus communis* L. (Pear) | | | | | | | | | | | |
| 1 | Seed | TLC | 30.1 | 13.8 | 2.4 | 29.3 | 2.7 | 5.5 | 3.1 | 0.2 | 1639 |
| | | | also LPC 3.8, LPE 3.1 | | | | | | | | |
| 2 | Fruit, flesh (1) | TLC | 11.3 | 35.4 | 29.9 | 2.4 | 5.3 | 3.1 | 7.0 | 0.111 | 1933 |
| | Fruit, flesh (2) | TLC | 24.5 | 35.4 | 32.1 | 3.4 | 3.8 | | | 0.045 | |
| | | | also LPC 2.2 (1), 0.5 (2); LPE 2.4 (1), 1.4 (2) | | | | | | | | |
| 2 | –, peel (1) | TLC | 16.7 | 39.6 | 29.2 | 2.8 | 4.2 | 2.1 | 3.5 | 0.099 | 1933 |
| | –, peel (2) | TLC | 22.3 | 43.7 | 27.2 | 1.9 | 3.8 | | | 0.206 | |
| | | | also LPC 0.7 (1), 1.0 (2); LPE 1.4 (1), 1.5 (2) | | | | | | | | |
| *Pyrus pyrifolia* ssp. *culta* (Mak.) Nakai (Nashi) | | | | | | | | | | | |
| 4 | Seed, kernel | TLC | 27.9-30.3 | 40.3-42.3 | | | 24.8-25.6 | 0.3-0.8 | | (LPC 0.9-1.3) | 1934 |
| 4 | –, coat | TLC | 23.4-24.5 | 45.3-47.2 | | | 25.2-26.8 | 0.3-0.6 | | (LPC 0.5-0.9) | 1934 |
| *Quercus palustris* Muenchh. (Pin Oak) | | | | | | | | | | | |
| 1 | Leaf | TLC | 33.5 | 30.6 | 3.5 | 1.3 | | | 31.1 | 0.37 | 1935 |
| *Quercus robur* L. (English Oak) | | | | | | | | | | | |
| 1 | Leaf | TLC | 15.4 | 21.2 | 25.8 | 9.1 | 10.6 | | 18.2 | 4.16[l] | 1936 |
| *Ramonda nathaliae* Panc. and Petrov | | | | | | | | | | | |
| 1 | Leaf | TLC | 52.2 | 21.7 | | | | | | 0.69[c] | 1937 |
| *Ramonda serbica* Panc. | | | | | | | | | | | |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Leaf | TLC | 51.0 | 21.6 | | | | | | 0.51[c] | 1937 |
| *Ranunculus glacialis* L. (Glacier Buttercup) | | | | | | | | | | | |
| 1 | Leaf | TLC | 41 | 18 | 34 | 6 | | | 0.9 | 0.13 | 1441 |
| *Raphanus acanthisformis* Becker (Japanese Radish) | | | | | | | | | | | |
| 1 | Leaf | TLC | | | | | + | | | | 1450 |
| *Raphanus sativus* L. (Radish) | | | | | | | | | | | |
| 1 | Seed | TLC | | | | | | $P_{NAPE}/P_{total}$ | 0.5 mg/seed | | 1497 |
| 1 | Seed | CC (silica) | 15.7 | 72.5 | | | | | | | 1536 |
| 1 | Leaf[a] | TLC | 3.6 | 8.3 | 5.4 | 1.7 | | | | | 1938 |
| 1 | Cotyledon, thylakoid[m] | TLC | 118 | | 467 | | | | | | 1939 |
| 1 | –, LHC(II) complex[m] | TLC | 11 | | 174 | | | | | | 1939 |
| *Raphanus sativus* L. ssp. *radicola* DC | | | | | | | | | | | |
| 1 | Leaf | TLC | 24 | 16 | 36 | 14 | | | 9 | | 1940 |
| *Raphia farinifera* (Gaertn.) Hyl. (Raffia Palm) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | + | | | | | 1941 |
| 1 | Fruit, mesocarp | TLC | + | | | + | | | | | 1941 |
| 1 | Pollen | TLC | + | + | | + | | | | | 1941 |
| *Raphia hookeri* Mann and Wendl. (Ivory Coast Raffia Palm) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | + | | | | | 1941 |
| 1 | Fruit, mesocarp | TLC | + | | | + | | | | | 1941 |
| 1 | Pollen | TLC | + | + | | + | | | | | 1941 |
| *Raphia regalis* Becc. | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | + | | | | | 1941 |
| 1 | Fruit, mesocarp | TLC | + | | | + | | | | | 1941 |
| 1 | Pollen | TLC | + | + | | + | | | | | 1941 |
| *Raphia sudanica* Chev. | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | + | | | | | 1941 |
| 1 | Fruit, mesocarp | TLC | + | | | + | | | | | 1941 |
| 1 | Pollen | TLC | + | + | | + | | | | | 1941 |
| *Raphia vinifera* Beauv. (Wine palm) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | + | | | | | 1941 |
| 1 | Fruit, mesocarp | TLC | + | | | + | | | | | 1941 |
| 1 | Pollen | TLC | + | + | | + | | | | | 1941 |
| *Rauvolfia serpentina* (L.) Benth. ex Kurz (Indian Snakeroot) | | | | | | | | | | | |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Cell culture | TLC | 55.0 | 20.1 | 2.0 | 10.2 | | 2.5 | | 1.53[e] | 1495 |
| *Rhaponticum integrifolium* C. Winkl. | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 1.0 | 794 |
| *Rhododendron* spp. (Rhododendron) | | | | | | | | | | | |
| 1 | Root[c,n] | TLC | 0.34 | + | + | + | | 0.45 | | | 1942 |
| *Ribes nigrum* L. (Black Currant) | | | | | | | | | | | |
| 1 | Seed[e] | TLC | 34.7 | 11.2 | 6.9 | 20.6 | 1.9 | 7.5 | 0 | (LPC 8.3, LPE 6.4) | 1487 |
| *Riccia fluitans* L. (Crystalwort) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 33.3 | 16.1 | 26.3 | 6.2 | 15.7 | | | 1.73[c] | 1551 |
| *Ricinus communis* L. (Castor Bean) | | | | | | | | | | | |
| 1 | Seed | TLC | 15.1 | 12.2 | | 19.2 | 13.8 | (LPC 3.1, LPE 3.8) | | 0.12[a] | 1943 |
| 1 | Seed, endosperm | TLC | | | | | | | (NAPE +) | | 1361 |
| 1 | –, glyoxysome | TLC | 51.4 | 27.2 | 2.7 | 9.0 | 1.5 | | 2.3 | | 1944 |
| 1 | –, endoplastic reticulum | TLC | 45.3 | 28.7 | 3.6 | 13.1 | 2.3 | | 2.5 | 1.24[h] | 1944 |
| 1 | –, proplastid | TLC | 35.6 | 38.7 | 8.4 | 8.0 | 4.6 | | | 0.55[h] | 1944 |
| 1 | –, mitochondria | TLC | 33.1 | 35.7 | 2.2 | 3.9 | 2.2 | | 17.7 | 0.65[h] | 1944 |
| 1 | –, spherosomes | TLC | 30 | 26 | 25 | 5 | 5 | | (LPC 0, LPE 0) | 0.38[a,c] | 1945 |
| 1 | Leaf[s] | TLC | 18.4 | 10.1 | 14.9 | | | | | | 1946 |
| 1 | Leaf | TLC | | | | | + | | | | 1450 |
| *Robinia pseudoacacia* L. (Black Locust) | | | | | | | | | | | |
| 1 | Leaf | TLC | 40 | 24 | 28 | 8 | | | | | 1607 |
| 1 | Bark | TLC | + | + | | | | (PC/PE ratio 1.5) | | | 1947 |
| *Roemeria refracta* DC (Roemer Poppy) | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 0.5 | 794 |

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*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Rorippa amphibia* (L.) Bess (Amphibious Marsh Cress) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 12.0 | 25.1 | 12.8 | 12.5 | 8.1 | 5.2 | 13.7 | 33.5 | 1789 |
| *Rosa canina* L. (Dog Rose) | | | | | | | | | | | |
| 1 | Seed[e] | TLC | 46.3 | 12.2 | 1.2 | 20.7 | 1.7 | 4.3 | 0.9 | | 1487 |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 0.2 | 794 |
| *Rosa rugosa* Thunb. (Turkestan Rose) | | | | | | | | | | | |
| 1 | Hips, chromoplast tubules | TLC | 27-40 | 19-20 | 6-9 | 24-28 | 17-19 | | | | 1948 |
| 1 | Leaf | TLC | 48 | 18 | 19 | 9 | | | 6 | 3.12[l] | 1523 |
| *Rubus* spp. (Blackberry) | | | | | | | | | | | |
| 2 | Callus culture | TLC | + | + | + | + | | | | | 1949 |
| 1 | Fruit | Frac. pptn. | 0.128 | | | | | | | | 1921 |
| *Rumex acetosa* L. (Sorrel) | | | | | | | | | | | |
| 1 | Leaf | TLC | 39.6 | 21.3 | 20.9 | 6.8 | 5.9 | 1.9 | 3.6 | 0.033 | 1761 |
| *Ruta graveolens* L. (Rue) | | | | | | | | | | | |
| 1 | Plant, aerial parts | TLC | 22.5 | 23.1 | 27.7 | 19.1 | 2.3 | 5.3 | Trace | 24.7[a] | 1950 |
| 1 | Shoot, leaf tissue culture | TLC | 12.8 | 30.1 | 32.9 | 16.5 | 2.1 | 5.5 | Trace | 17.7[a] | 1950 |
| *Saccharum officinarum* L. (Sugarcane) | | | | | | | | | | | |
| 1 | Leaf | TLC | 19.4 | 19.1 | 41.0 | 10.2 | 5.3 | 2.0 | | 1.89[c] | 1951 |
| 1 | Juice, raw | TLC | 36.7 | 28.3 | | | | | | 7.15[w] | 1952 |
| 1 | Suspension culture | TLC | 3.0 | 33.2 | 42.2 | 11.6 | 4.8 | 2.1 | | 1.86[c] | 1951 |
| *Sagittaria sagittifolia* L. (Swamp Potato) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 42.7 | 10.9 | 21.9 | 7.1 | 5.3 | 12.1 | | 2.30[c] | 1445 |
| *Salicornia arabica* L. | | | | | | | | | | | |
| 1 | Shoot | TLC | 43.0 | 5.1 | 11.0 | 6.8 | | 8.0 | 19.0 | 0.235[c] | 1488 |
| *Salicornia europaea* L. (Samphire) | | | | | | | | | | | |
| 1 | Leaf | TLC | 50.0 | 10.1 | 9.1 | | | | | 3.35[c] | 1494 |
| 1 | Root | TLC | 54.0 | 24.0 | Trace | | | | | 0.10[c] | 1494 |
| *Salix herbacea* L. (Dwarf Willow) | | | | | | | | | | | |
| 1 | Leaf | TLC | 44 | 17 | 31 | 7 | | | 1 | 0.44 | 1441 |
| *Salix reticulata* L. (Netleaf Willow) | | | | | | | | | | | |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Leaf | TLC | 51 | 19 | 19 | 8 | | | 2 | 0.25 | 1441 |
| *Salix retusa* L. (Notchleaf Willow) | | | | | | | | | | | |
| 1 | Leaf | TLC | 52 | 21 | 18 | 7 | | | 1 | 0.28 | 1441 |
| *Salvadora oleoides* Decne (Khakan) | | | | | | | | | | | |
| 1 | Seed | TLC | 17.1 | 29.9 | | 27.3 | | | 22.7 | | 1953 |
| *Salvinia nutans* (L.) Allioni | | | | | | | | | | | |
| 1 | Whole plant | TLC | 28.0 | 18.6 | 13.2 | 10.6 | 8.0 | 7.2 | 14.4 | 18.4 | 1789 |
| *Sambucus nigra* L. (European Elder) | | | | | | | | | | | |
| 1 | Leaf | PC | 43 | 11 | 39 | 7 | | | | | 1517 |
| *Sapium sebiferum* (L.) Roxb. (Vegetable Tallow Tree) | | | | | | | | | | | |
| 1 | Seed | TLC | 45.3 | 12.9 | Trace | 16.7 | 7.7 | | | 0.7[c] | 1954 |
| | | | also NAPE 6.2, NALPE trace, LPC 5.3, LPE trace | | | | | | | | |
| *Saponaria vaccaria* L. (Cow Cockle) | | | | | | | | | | | |
| 1 | Seed, whole | TLC | 37 | 19 | | 27 | 12 | 0.4 | | (LPC 2.3, LPE 1.5) | 1955 |
| 1 | –, dehulled | TLC | 41 | 7 | | 34 | 11 | 0.9 | | (LPC 2.6, LPE 5.0) | 1955 |
| 1 | –, starch | TLC | 15 | 8 | | | | 13 | | (LPC 52, LPE 11) | 1956 |
| *Saussuria depressa* (L.) DC | | | | | | | | | | | |
| 1 | Leaf | TLC | 48 | 19 | 20 | 11 | | | 2 | 0.11 | 1441 |
| *Saxegothaea conspicua* Lindl. (Prince Albert Yew) | | | | | | | | | | | |
| 1 | Needle | TLC | 14 | 19 | 33 | 33 | | | | 2.1[o] | 1915 |
| *Secale cereale* L. (Rye) | | | | | | | | | | | |
| 4 | Seed grain[a] | TLC | 4-5 | <3 | | <3 | | | (NAPE +, LPC +) | | 1957 |
| 1 | Seed nucleus, diploid | TLC | + | + | | | | | | 61.6[a] | 1958 |
| 1 | –, tetraploid | TLC | + | + | | | | | | 61.8[a] | 1958 |
| 1 | Seed embryo | TLC | 34.8 | 35.3 | | 29.8 | | | | | 1959 |
| 1 | –, nuclear matrix | TLC | 32.1 | 56.0 | | 11.9 | | | | | 1960 |
| 1 | Starch | TLC | | | | | | (LPC 51.9) | | 0.54[d] | 1499 |
| 2 | Leaf | TLC | 25.4-36.5 | 12.3-12.9 | 48.6-25.2 | 10.2-17.0 | | | 3.5-8.3 | 11.4-14.0[a] | 1961 |
| 1 | –, thylakoid | TLC | | | 11 | | | | | | 1440 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, plasma membrane | TLC | 46.7 | 34.5 | 5.8 | 2.2 | 4.5 | 5.4 | | 1.07[h] | 1962 |
| 1 | –, LHC (II) complex[a] | TLC | 7 | 2 | 33 | | | | | | 1963 |
| 1 | Leaf, chloroplast envelope, inner membrane | TLC | 8.1 | 0.2 | 4.0 | 0.7 (incl. PS) | | 1.3 | | | 1964 |
| 1 | –, outer membrane | TLC | 31.5 | 0.7 | 5.0 | 4.5 (incl. PS) | | 1.5 | | | 1964 |
| 2 | Shoot, tillering node | TLC | 26.7-37.2 | 15.3-22.5 | 23.2-15.4 | 11.6-8.3 | | | 23.3-16.6 | 30.2-23.6[a] | 1961 |
| 1 | Shoot, plasma membrane[j] | HPLC | 73.5 | 109.7 | | | | | | | 1505 |
| 1 | Root | TLC | 60 | 23 | 6 | 5 | | 3 | 3 | 0.24 | 1965 |
| 1 | Seedling | PC | 56.5 | 16.7 | | | 21.1 | | | 0.48 | 1355 |
| *Selaginella kraussiana* (Kunze) A. Braun | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Selaginella pallescens* (C. Presl.) Spring (Moss Fern) | | | | | | | | | | | |
| 1 | whole plant | TLC | + | + | | | | | | | 1436 |
| *Selaginella selaginoides* (L.) P. Beauv. (Club Spikemoss) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Selaginella uncinata* (Desv. ex Poir.) Spring (Blue Spikemoss) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Selaginella willdenowii* (Desv. ex Poir.) Baker | | | | | | | | | | | |
| 1 | ''''Whole plant | TLC | + | + | | | | | | | 1436 |
| *Senecio vulgaris* L. (Groundsel) | | | | | | | | | | | |
| 1 | Leaf, thylakoid[a] | TLC | | | 11.5 | | | | | | 1913 |
| 1 | –, chloroplast | HPLC | 36.0 | 36.8 | 8.6 | 7.1 | | 11.5 | | 77.1[a] | 1465 |
| *Senna septentrionalis* (Viv.) Irwin and Barn. (Arsenic Bush) | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.33 | | | | | | 1402 |
| *Sequoiadendron giganteum* (Lindl.) Buchh. (Giant Sequoia) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | | | | | | | 1436 |
| *Sesamum indicum* L. (Sesame) | | | | | | | | | | | |
| 1 | Seed | TLC | 14.0 | 57.5 | 7.3 | 11.9 | | 4.1 | 5.0 | 41.54 | 1446 |
| 3 | Seed[n] | TLC | 13.9-16.1 | 3.7-5.9 | | 5.7-6.8 | | | | | 1966 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Seed, oil body | TLC | 41.2 | 15.8 | | 20.9 | 22.1 | | | 0.57 | 1482 |
| *Setaria glauca* (L.) Beauv. (Yellow Foxtail) | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.72 | | | | | | 1402 |
| *Setaria italica* (L.) Beauv. (Italian Foxtail Millet) | | | | | | | | | | | |
| 1 | Seed, glutinous | TLC | + | + | + | + | | | + (LPC +) | 0.08 | 1967 |
| *Setaria verticillata* (L.) Beauv. (Bristly Foxtail) | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.79 | | | | | | 1402 |
| *Sicyos angulatus* L. (Bur Cucumber) | | | | | | | | | | | |
| 2 | Leaf | TLC | | | 4.17-4.54[a] | | | | | 3.66-3.75[l] | 1628 |
| *Simmondsia chinensis* (Link) Schneid. (Jojoba) | | | | | | | | | | | |
| 1 | Seed | TLC | 45 | 38 | 7 | 10 | | | | 0.16 | 1968 |
| 1 | Leaf, chloroplast | TLC | 29 | | 50 | 21 | | | | | 1969 |
| 1 | –, tissue | TLC | 58 | 20 | 14 | 2 | | | | | 1970 |
| 1 | –, protoplast | TLC | 24 | 13 | 10 | 13 | | | | | 1970 |
| 1 | Callus, tissue | TLC | 41 | 25 | 3 | 21 | | | | | 1970 |
| 1 | –, protoplast | TLC | | 27 | 5 | 32 | | | | | 1970 |
| 1 | Explant, shoot | TLC | 19[a] | | | | | | | 1.59[e] | 1971 |
| 1 | –, callus | TLC | 20[a] | | | | | | | 0.82[e] | 1971 |
| *Sison amomum* L. (Stone Parsley) | | | | | | | | | | | |
| 1 | Seed | TLC | 21 also LPC 6, LPE 1 | 4 | 2 | 33 | | 22 | 2 | 1.1[a] | 1438 |
| *Smilax* spp. (Greenbrier) | | | | | | | | | | | |
| 1 | Leaf | TLC | | | 7 | | | | | | 1440 |
| *Solanum acaule* Bitt. (Wild Potato) | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | 1.28 | 1.06 (incl. PG) | | 0.13 | | | | | 1972 |
| *Solanum acaule* Bitt. ssp. *depexum* Buk. | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | + | + | | | | | 1786 |
| *Solanum acaule* Bitt. ssp. *punae* Juz. | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | 1.30 | 1.09 (incl. PG) | | 0.10 | | | | | 1972 |
| *Solanum acaule* Bitt. ssp. *schreiteri* Buk. | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | 1.23 | 0.92 (incl. PG) | | 0.15 | | | | | 1972 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]µmol PL/mg protein; [i]µmol PL/mg chlorophyll; [j]µg PL/mg protein; [k]µg lipid P/g; [l]µmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]µmol PL/g dwb; [p]µg PL/100 mg fwb; [q]µg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]µmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]µg PL/mL; [x]µg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]µg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]µg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Solanum argentinum* Bitter and Lillo | | | | | | | | | | | |
| 1 | Seed | TLC | 17.4 | 20.2 | | | | (Sphingo-PL 20.5) | | | 1973 |
| *Solanum commersonii* Dun. (Commerson's Nightshade) | | | | | | | | | | | |
| 1 | Leaf, plasma membrane | TLC | 42.6 | 36.2 | 3.7 | 5 (incl. LPE) | | 9.5 | (LPC 2.6) | 48.3[a] | 1974 |
| *Solanum demissum* Lindl. (Nightshade) | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | 1.21 | 1.16 (incl. PG) | | 0.09 | | | | | 1972 |
| *Solanum maglia* Schlecht | | | | | | | | | | | |
| 1 | Leaf | TLC | 9.1 | 10.9 | 79.9 | 0.1 | | | | 0.206 | 1975 |
| *Solanum melongena* L. (Eggplant) | | | | | | | | | | | |
| 1 | Seed | HPLC | 29.3 | 19.1 | | 10.5 | | 41.0 | | 28.8[k] | 1976 |
| 1 | Leaf[l] | TLC | 0.635 | | | | | | | | 1514 |
| 1 | Fruit[l] | TLC | 0.092 | | | | | | | | 1514 |
| 1 | Fruit | TLC | 0.3 | 0.9 | 6.6 | | (LPC 0.2) | 0.6 | 90.4 | 0.205 | 1446 |
| *Solanum pamitanae* | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | 0.46 | 0.77 (incl. PG) | | 0.11 | | | | | 1972 |
| *Solanum rybinii* Juz. et Buk. | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | 1.28 | 1.04 (incl. PG) | | 0.11 | | | | | 1786,1972 |
| *Solanum sanctae-rosae* Hawkes | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | 0.54 | 0.60 (incl. PG) | | 0.12 | | | | | 1972 |
| *Solanum schreiteri* Buk. (Wild Potato) | | | | | | | | | | | |
| 1 | Leaf, chloroplast | TLC | 29.7 | | 39.9 | 9.1 | | 21.3 | | 0.026[l] | 1977 |
| *Solanum tuberosum* L. (Potato) | | | | | | | | | | | |
| 1 | Leaf | TLC | 50.2 | 13.4 | 21.7 | 10.5 | 1.1 | 1.4 | 1.8 | 2.77[l] | 1978 |
| 1 | Leaf[a] | HPLC | 7.9 | 4.3 | 2.9 | 0.6 | 0.6 | 0 | 0 | | 1413 |
| 1 | –, plasma membrane | TLC | 38.4 | 35.7 | 3.9 | | 7.5 (incl. LPE) | 10.2 | (LPC 4.3) | 46.4[a] | 1974 |
| 1 | Tuber, peeled[a] | TLC | 25.8 | 12.6 | 0.9 | 6.3 | 0.6 | 0.3 | 0.6 | 47.4 | 1979 |
| 1 | Tuber | TLC | 41.5 | 32.1 | | 26.4 | | | | 0.046 | 1980 |
| 4 | Tuber, free | TLC | 45.4-46.9 | 35.4-36.1 | | 17.8-18.5 | | | | 5.2-8.6[a] | 1981 |
| 4 | –, bound | TLC | 23.8-29.3 | 42.7-44.9 | 11.1-12.3 | 14.7-16.3 | | | | 32.7-34.7[a] | 1981 |
| 1 | Tuber[a] | HPLC | 15.9 | 33.6 | 0.4 | 2.5 | 1.4 | 0 | 0 | | 1413 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Tuber[l] | Choline | 14 | | | | | | | | 1451 |
| 1 | Tuber, mitochondria | TLC | 44.3 | 26.3 | | 12.7 | | | 16.8 | 0.0277 | 1982 |
| 1 | –, inner membrane | TLC | 27 | 29 | | 24.5 | | | 19.5 | | 1982 |
| 1 | –, outer membrane | TLC | 52.6 | 25.0 | | 10.3 | | | 12.1 | | 1982 |
| 1 | –, microsomes | TLC | 44.3 | 17.6 | | 19.1 | | | 19.0 | 0.0292 | 1982,1983 |
| 1 | Tuber, cell wall | TLC | 35.1 | 33.0 | | 31.9 | | | | 0.0009 | 1984 |
| 1 | –, peroxisome | TLC | 52.5 | 20.9 | | 7.2 | | | 2.9 | 0.0014 | 1984 |
| 1 | –, plasmalemma | TLC | 60.4 | 22.9 | | 10.3 | | | 6.3 | 0.0041 | 1984 |
| 1 | –, starch | TLC | 73.0 | 15.3 | | 11.6 | | | | 0.0001 | 1984 |
| 1 | Tuber, plasmalemma | TLC | 33.1 | 39.3 | | 14.6 | 2.7 | 5.0 | 2.1 | (LPC 3.2) | 1985 |
| 1 | Starch | TLC | + | 0 | | | + | | | (LPC 0, LPE 0, LPS 0) | 1902 |
| 1 | Starch | TLC | + | | + | | | | | 0.006 | 1986 |
| *Sophora japonica* L. (Japanese Pagoda Tree) | | | | | | | | | | | |
| 1 | Seed | TLC | 38.5 | 15.1 | 5.9 | 20.1 | 0 | 1.2 | | 1.1 | 1987,1988 |
| | | | also NAPE 6.8, NALPE 2.1, LPC 2.3 | | | | | | | | |
| 1 | Bud | TLC | 20.3 | 14.0 | 13.9 | 17.0 | 0 | 16.0 | | 0.28 | 1987 |
| | | | also NAPE 9.1, NALPE 6.8, LPC 2.9 | | | | | | | | |
| 1 | Flower | TLC | 22.0 | 19.2 | 8.2 | 19.2 | 0 | 15.1 | | 0.6 | 1987 |
| | | | also NAPE 7.3, NALPE 3.0, LPC 4.0 | | | | | | | | |
| *Sorbus aucuparia* L. (Rowan) | | | | | | | | | | | |
| 1 | Leaf | TLC | 40 | 31 | 18 | 7 | | | 5 | 5.54[l] | 1523 |
| *Sorghum bicolor* (L.) Moench. (Sorghum) | | | | | | | | | | | |
| 1 | Seed | TLC | 36.3 | 5.5 | 1.2 | Trace | Trace | 1.6 | | 0.93[c] | 1989 |
| | | | also LPC 41.8, LPE 13.6 | | | | | | | | |
| 1 | Leaf, chloroplast | TLC | 26 | 4 | 48 | 13 | 4 | | 4 | | 1990 |
| 1 | Root | TLC | 46.8 | 30.2* | 10.0 | 2.1 | | 5.0 | 5.2 | | 1699 |
| | *Incl. PS | | | | | | | | | | |
| *Sorghum bicolor* L. var. *cernuum* Host. (White Durra) | | | | | | | | | | | |
| 1 | Grain | TLC | | + | | + | + | | | 0.59 | 1991 |
| *Spartina patens* (Ait.) Muhl. (Saltmeadow Cordgrass) | | | | | | | | | | | |
| 1 | | TLC | 8.5 | 6.1 | 2.2 | 1.1 | 1.0 | | | 20.5[c] | 1992 |

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*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Root plasma membrane[a] | | | | | | | | | | |
| *Sphagnum nemoreum* Scop. | | | | | | | | | | | |
| 1 | Whole plant | TLC | 14.9 | 26.2 | 35.4 | 12.1 | 11.2 | | | 0.22[c] | 1493 |
| *Sphagnum palustre* L. (Prairie Sphagnum) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Sphagnum squarrosum* Crome (Sphagnum) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 11.3 | 32.7 | 34.7 | 8.1 | 13.2 | | | 0.06[c] | 1493 |
| *Spinacia oleracea* L. (Spinach) | | | | | | | | | | | |
| 1 | Leaf | TLC | 28.9 | 14.2 | 39.1 | 3.9 | 3.1 | 4.8 | 6.0 | 0.105 | 1761 |
| 1 | Leaf[a] | HPLC | 14.0 | 8.6 | 7.4 | 2.9 | 0 | 0 | 1.7 | | 1413 |
| 3 | Leaf[l] | Choline | 66-141 | | | | | | | | 1451 |
| 1 | Leaf | PC | 56 | 17 | 16 | 11 | | | | | 1517 |
| 1 | –, chloroplast | PC | 39 | 2 | 46 | 13 | | | | | 1517 |
| 1 | –, chloroplast | TLC | 28 | 67 | 6 | | | | | | 1969 |
| 1 | –, plasma membrane | TLC | 25.4 | 24.4 | 3.1 | | | 6.1 | | | 1993 |
| 1 | –, mitochondria | TLC | 45 | 39 | 4 | 1 | | | 11 | | 1994 |
| 1 | –, lamellae | TLC | 24 | 0 | 65 | 11 | | | | 14,200[q] | 1995 |
| 1 | –, lamellae[f] | CC (DEAE) | 55 | 0 | 157 | 28 | | | | | 1379 |
| 1 | –, PS (II) fraction[g] | TLC | 3 | | 9 | | | | | | 1996 |
| 1 | –, thylakoid[d] | TLC | 0 | | 7 | 2 | | | | 49[f] | 1997 |
| 1 | Leaf chloroplast envelope[g] | TLC | 18 | 0 | 9 | 2 | | | 0 | | 1998 |
| 1 | –, inner membrane[d] | TLC | Trace | | 7 | 3 | | | | 107[f] | 1997 |
| 1 | –, outer membrane[g] | TLC | 32 | 0 | 10 | 5 | | | 0 | | 1998 |
| 1 | Leaf, inner envelope | HPLC | | | + | | | | | | 1999 |
| 1 | –, outer envelope | HPLC | | | + | | | | | | 1999 |
| 1 | –, thylakoid | HPLC | | | + | | | | | | 1999 |
| 1 | Petiole, mitochondria | TLC | 39 | 42 | 2 | 2 | | | 12 | | 1994 |
| 1 | Root | TLC | 62.4 | 32.1 | Trace | | | | | 1.14[c] | 1494 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Root | TLC | 33.7 | 16.3 | | | 49.5 | | | 9.5[g] | 2000 |
| *Spirodela oligorrhiza* (Kurz) Hegelm. (Duckweed) | | | | | | | | | | | |
| 1 | Whole tissue | TLC | 42.4 | 20.3 | 14.9 | 6.8 | 1.5 | 0.7 | | 3.22[l] | 1389 |
| 1 | Leaf, chloroplast | TLC | 34.3 | 5.3 | 36.9 | 9.4 | 1.2 | 1.6 | | | 1389 |
| *Spirodela polyrrhiza* (L.) Schleid. (Giant Duckweed) | | | | | | | | | | | |
| 1 | Frond | TLC | 56 | 21 | 18 | 6 | | | | | 2001 |
| 1 | Leaf, chloroplast | TLC | 20 | | 80 | | | | | | 2002 |
| *Sterculia foetida* L. (Indian Almond, Jangli Badam) | | | | | | | | | | | |
| 1 | Nut, kernel | TLC | 30.0 | 23.0 | | 40.6 | | | | 0.2 | 1548 |
| *Striga asiatica* (L.) Kuntze (Witchweed) | | | | | | | | | | | |
| 1 | Seed | TLC | 12 | 17 | 29 | 27 | | | | | 2003 |
| *Striga aspera* (Willd.) Benth. | | | | | | | | | | | |
| 1 | Leaf, chloroplast[g] | TLC | 10 | | 30 | | | | | | 2004 |
| *Striga hermonthica* (Del.) Benth. (Purple Witchweed) | | | | | | | | | | | |
| 1 | Leaf, chloroplast[g] | TLC | 10 | | 32 | | | | | | 2004 |
| *Suaeda fruticosa* Forsk. (Alkali Seepweed) | | | | | | | | | | | |
| 1 | Shoot | TLC | 54.3 | 15.0 | 8.7 | 3.9 | | 9.4 | 4.7 | 0.127[c] | 1488 |
| *Suaeda maritima* (L.) Dum. | | | | | | | | | | | |
| 1 | Leaf, protoplast and tonoplast | TLC | + | + | | + | + | | | | 2005 |
| *Suaeda maritima* ssp. *macrocarpa* (Annual Seablite) | | | | | | | | | | | |
| 1 | Leaf | TLC | 59.0 | 20.9 | 16.1 | 4.1 | | | | | 2006 |
| 1 | –, chloroplast memb. | TLC | 39.9 | | 48.0 | 12.1 | | | | 22.3[q] | 2007 |
| *Swietenia mahogoni* Jacq. (West Indian Mahogany) | | | | | | | | | | | |
| 1 | Seed | TLC | 31.5 | 28.9 | 5.6 | 28.2 | | | 5.8 | 3.44[c] | 1429 |
| *Tamarindus indica* L. (Tamarind) | | | | | | | | | | | |
| 1 | Seed, kernel | TLC | ++ | ++ | | + | + | + | | (LPC +, LPE +) | 2008 |
| *Tapinanthus dodoneifolius* (DC) Danser (African Mistletoe) | | | | | | | | | | | |
| 1 | Leaf chloroplast[y] | TLC | 119 | | + | + | | | | 30 | 2009 |

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*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Taxus baccata* L. (English Yew) | | | | | | | | | | | |
| 1 | Leaf | TLC | + | + | | | | | | | 1436 |
| *Taxus cuspidata* Sieb. and Zucc. (Japanese Yew) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | | (LPC +) | | | | 2010 |
| *Tetragonia expansa* Thunb. (New Zealand Spinach) | | | | | | | | | | | |
| 1 | Leaf | CC (silica) | 28.6 | | | | | | | 1.16[l] | 1459 |
| 1 | Leaf | PC | + | + | | + | + | | | | 1816 |
| 1 | Leaf | PC | 59 | | 29 | 12 | | | | | 1746 |
| 1 | –, chloroplast | PC | 37 | 6 | 34 | 21 | | | | | 1746 |
| *Theobroma cacao* L. (Cocoa) | | | | | | | | | | | |
| 3 | Bean, shelled | TLC | 36.1-40.4 | 11.3-18.6 | | 25.5-29.0 | 2.3-3.3 | 0.6-3.7 | (LPC 4.5-9.0) | 0.28-0.45 | 2011 |
| 1 | Butter *Incl. LPE | TLC | 37.7 also LPC 8.0, LPE + | 15.6 | 27.3 | 10.9* | 0.3 | 0.2 | | 0.34[c] | 2012 |
| *Thevetia neriifolia* [Juss. ex] Steud. (Yellow Oleander, Pivala Kanher) | | | | | | | | | | | |
| 1 | Seed | TLC | 17.2 | 27.2 | | 30.1 | | | 24.0 | | 1550 |
| *Thuidium tamariscinum* (Hedw.) Schimp. (Tamarisk Thuidium Moss) | | | | | | | | | | | |
| 1 | Whole plant | TLC | + | + | | | | | | | 1436 |
| *Torreya nucifera* Sieb. and Zucc. (Kaya Nut) | | | | | | | | | | | |
| 1 | Seed | TLC | + | + | | | (LPC +) | | | | 2010 |
| *Trichodesma incanum* (Bunge) A. DC | | | | | | | | | | | |
| 1 | Seed, defatted | TLC | + | + | | + | | | | 0.1 | 794 |
| *Trichopilia tortilis* Lindl. | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.30 | | | | | | 1402 |
| *Trifolium alexandrinum* L. (Berseem Clover) | | | | | | | | | | | |
| 1 | Seed | TLC | | + | + | + | | + | (LPC +, LPE +) | | 2013 |
| *Trifolium pratense* L. (Red Clover) | | | | | | | | | | | |
| 1 | Seed | TLC | 20.1 | 14.6 | | 9.3 | 7.2 | 7.0 | 8.9 | | 2014 |
| 1 | Leaf | CC (DEAE) | 37 | 15 | 23 | 2 | | | | 0.22 | 2015 |
| *Trifolium repens* L. (White Clover) | | | | | | | | | | | |
| 1 | Leaf | TLC | 36 | 22 | 29 | 6 | | | 7 | 3.94[l] | 1523 |
| 1 | Root | TLC | 10.0 | 44.0 | 19.2 | 2.7 | | 24.1 | | 37.0[e] | 1448 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Trifolium* spp. (Hartshorn Clover) | | | | | | | | | | |
| 1 | Seed | TLC | 65 | 13 | | 22 | | | 0.46 | 1481 |
| *Trigonella corniculata* (L.) L. | | | | | | | | | | |
| 1 | Seed | TLC | 29.8 | 24.5 | 2.5 | 23.5 | | 19.7 | 0.13 | 1681 |
| *Trigonella foenum-graecum* L. (Fenugreek) | | | | | | | | | | |
| 1 | Seed | TLC | 54.6 | 29.5 | 2.6 | 3.2 | 4.1 | 2.2 (LPC 3.8) | 0.79[c] | 2016 |
| 1 | Leaf | TLC | 50.0 | 24.0 | 17.4 | + | + | | 21.2[a] | 2017 |
| 1 | Hypocotyl | TLC | + | + | + | + | + | | | 2017 |
| *Triticum aegilopoides* Bal. (Wild Einkorn) | | | | | | | | | | |
| 2 | Leaf, chloroplast[m] (1) | TLC | 0.07 | 0.26 | | | | | | 1437 |
| | Leaf, chloroplast[m] (2) | TLC | 0.08 | 0.24 | | | | | | |
| *Triticum aestivum* L. (Wheat) | | | | | | | | | | |
| 1 | Whole grain | HPLC | 26.2 | 19.7 | | Trace | Trace | 31.3 | 0.47 | 2018 |
| | | | also given: LPC 26.2, LPE 5.6 | | | | | | | |
| 14 | Seed | TLC | 10.6-12.6 | 1.9-3.2 | | | 1.7-2.4 | 20.9-26.8* | 0.68-0.80[g] | 2019 |
| | *Incl. a glycolipid | | also LPC 2.0-3.4 | | | | | | | |
| 1 | Flour | TLC | 25.4 | 3.5 | | 0.6 | 0.8 | | 0.032 | 2020 |
| | | | also NAPE 21.8, NALPE 12.8, LPC 29.6, LPE 4.0 | | | | | | | |
| 1 | Flour | CC (silica) | + | | | (NAPE +, NALPE +, LPC +) | | | | 2021 |
| 7 | Flour | TLC | 24.4-55.2 | Trace-34.2 | | | Trace-14.7 | | 0.06-0.13[c] | 2022 |
| 1 | Flour | TLC | + | + | | (LPC +, LPE +) | | | | 2023 |
| 1 | –, nonstarch | TLC | 29 | 6 | | + | | | | 1392 |
| | | | also NAPE 31, NALPE 15, LPC 16, LPE 4 | | | | | | | |
| 1 | Flour, nonstarch | HPLC | 6.2 | 31.2 | 17.9 | | | (NAPE 16.1) | | 1417 |
| 1 | –, starch | TLC | 5 | 1 | | + | | (LPC 86, LPE 8) | | 1392 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/cm$^2$ leaf area; [y]Molecules per 10$^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2 | –, starch | TLC | Variation of LPL content with granule size | | | | | | | | 2024 |
| 1 | Starch | HPLC | 1.1 | 0 | 0 | | | | | | 1417 |
| | | | also NAPE 0, NALPE 0, LPC 87.3, LPE 11.5, LPG 0.1 | | | | | | | | |
| 6 | Starch[cc] | HPLC | | | (LPC +) | | | | | | 2025 |
| 1 | Seed | TLC | 45.4 | 11.6 (incl. LPA) | + | | 3.3 | Trace | | 146[k] | 2026 |
| | | | also NAPE 11.0, NALPE 13.2, LPC 14.0, LPE 1.6 | | | | | | | | |
| 3 | –, kernel | TLC | 7.3-18.9 | 2.9-5.2 (incl. PG) | | 0-7.2 | | 0.9-18.5 | | 0.87-1.17 | 2027 |
| | | | also LPC 38.5-71.3, LPE 5.8-8.0, LPG 2.3-19.4, LPI-LPS 0-3.4 | | | | | | | | |
| 3 | –, germ | TLC | 44.4-60.4 | 15.7-16.2 (incl. PG) | | 15.0-18.9 | | | 1.3-4.1 | 0.11-0.15 | 2027 |
| | | | also LPC 2.4-6.2, LPE 2.4-2.8, LPI/LPS 0-8.8 | | | | | | | | |
| 3 | –, aleurone | TLC | 50.2-65.4 | 7.8-15.8 (incl. PG) | | 13.9-18.5 | | | 0.6-5.8 | 0.11-0.13 | 2027 |
| | | | also LPC 6.3-13.2, LPI/LPS 0.5-2.8 | | | | | | | | |
| 3 | –, nonstarch endosperm | TLC | 12.5-22.2 | 1.4-2.6 (incl. PG) | | | | | | 0.04-0.06 | 2027 |
| | | | also LPC 19.6-22.4, LPE 2.2-2.5, LPI/LPS 0.9-2.7 | | | | | | | | |
| 3 | –, starch endosperm | TLC | 0-0.5 | | | | | 0-2.4 | | 0.43-0.55 | 2027 |
| | | | also LPC 66.0-84.6, LPE 10.9-13.2, LPG 3.1-7.1, LPI-LPS 0.6-11.2 | | | | | | | | |
| 1 | –, spherosomes (from aleurone layer) | TLC | 67.4 | 16.8 | | 14.3 | | | | 8.9[c] | 2028 |
| 1 | Seed, chromatin | TLC | 48 | 18 | | 9 | 9 | (TLC 8) | 7 | 14.6[z] | 2029 |
| 1 | Grain, lipoprotein complex | TLC | 41.8 | 4.2 | 2.3 | 7.7 | | 1.8 | | 0.47 | 2030 |
| | | | also NAPE 11.6, LPC 15.7, LPE 0.5 | | | | | | | | |
| 1 | Leaf | TLC | 48.8 | 18.4 | 27.8 | 5.0 | | | | 1.54[m] | 1579 |
| 1 | Leaf | TLC | 23.6 | 19.3 | 43.2 | 12.1 | 0.5 | | 1.2 | 160.3[j] | 2031 |
| 6 | Leaf | TLC | | | 13-16 | | | | | | 1440 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 11 | Leaf | TLC | 20.5-32.1 | 21.3-26.7 | | | | | | 1.30-2.91 | 2032 |
| 2 | –, thylakoid | TLC | | | 18 | | | | | | 1440 |
| 1 | –, chloroplast | TLC | 29 | 5 | 48 | 10 | 5 | | 5 | | 1990 |
| 1 | –, envelope | TLC | 57.2 | 7.2 | 25.0 | 9.2 | | | | 15.2[a] | 2033 |
| 1 | –, thylakoid | TLC | 24.8 | 0 | 57.4 | 14.0 | | | | 12.9[a] | 2033 |
| 1 | Leaf, stroma lamellae[a] | TLC | 2.4 | | 10 | | | | | | 2034 |
| 1 | –, grana[a] | TLC | 1.4 | | 8.6 | | | | | | 2034 |
| 1 | Tillering node | TLC | 44.9 | 16.9 | 17.6 | 6.2 | 4.9 | | 9.5 | 121.1[j] | 2031 |
| 1 | Leaf, protein concentrate[g] | TLC | 0 | 3.5 | | | | | | 3.5[g] | 2035 |
| 1 | Bran<br>*Incl. LPE | TLC | 28.4 | 5.2 | 2.2 | 11.2 | 4.6* | 4.0 | 1.7 | | 1393 |
| | | | also NAPE 5.9, NALPE 13.6, LPC 30.4 | | | | | | | | |
| 1 | Starchy endosperm<br>*Incl. LPE | TLC | 2.9 | 0.5 | 0 | 1.0 | 8.6* | 0 | 0 | | 1393 |
| | | | also NAPE 7.8, NALPE 6.4, LPC 66.6 | | | | | | | | |
| 1 | Seedling | PC | 51.2 | 15.7 | | | 24.1 | | | 0.53 | 1355 |
| 1 | Root<br>*Incl. PS | TLC | 46.9 | 33.2* | 6.4 | 2.1 | | 5.3 | 5.6 | | 1699 |
| 1 | Root | HPLC | 51 | 35 | 4 | 6 | 4 (incl. PA) | | | 0.827[e] | 1407 |
| 1 | –, microsomal membrane[a] | TLC | 40.4 | 14.6 | 4.1 | 1.4 (incl. PS) | | 1.6 | | | 2036 |
| 1 | –, plasma membrane[a] | TLC | 42.1 | 27.2 | 6.6 | 10.8 | 2.4 | 5.2 | | | 2037 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]µmol PL/mg protein; [i]µmol PL/mg chlorophyll; [j]µg PL/mg protein; [k]µg lipid P/g; [l]µmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]µmol PL/g dwb; [p]µg PL/100 mg fwb; [q]µg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]µmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]µg PL/mL; [x]µg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]µg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]µg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Root, whole[l] | Choline | 0.23 | | | | | | | 0.98 | 1506 |
| | | | Data also given for cell wall, mitochondria, and microsomes | | | | | | | | |
| 1 | Tillering nodes | TLC | 30.9 | 13.8 | 5.6 | 8.1 | 3.0 | 11.7 | 3.2 | | 2038 |
| 1 | –, mitochondria | TLC | 20.9 | 15.3 | 1.9 | 3.6 | | | 1.0 | 7.03 | 2039 |
| *T. aestivum* L. × *Secale cereale* L. (Triticale) | | | | | | | | | | | |
| 1 | Seed | TLC | 64.4 | 16.4 | | 5.2 | 14.2 | | (LPC trace) | | 2040 |
| *Triticum compactum* Host. (Club Wheat) | | | | | | | | | | | |
| 1 | Seed<br>*Incl. a glycolipid | TLC | 9.5 | 2.8 | | | 2.5 | 21.2* | (LPC 3.0) | 0.75[g] | 1864 |
| *Triticum dicoccoides* Körn. (Wild Emmer) | | | | | | | | | | | |
| 2 | Leaf, chloroplast[m] | TLC | 0.08 | | 0.21 | | | | | | 1437 |
| *Triticum dicoccum* Schrank (Emmer) | | | | | | | | | | | |
| 2 | Leaf, chloroplast[m] (1) | TLC | 0.10 | | 0.23 | | | | | | 1437 |
| | Leaf, chloroplast[m] (2) | TLC | 0.06 | | 0.23 | | | | | | |
| *Triticum durum* Desf. (Durum Wheat) | | | | | | | | | | | |
| 1 | Whole grain | HPLC | 21.5 | 25.2 | | Trace | Trace | 28.0 | | 0.47 | 2018 |
| | | | also LPC 21.5, LPE 11.2 | | | | | | | | |
| 1 | Seed, kernel | TLC | 17.0 | 3.4 (incl. PG) | | 6.1 | | | 1.8 | 1.13 | 2027 |
| | | | also LPC 53.4, LPE 6.2, LPG 2.6 | | | | | | | | |
| 1 | –, germ | TLC | 55.5 | 15.0 | 1.2 | 13.8 | | (LPC 11.5) | 3.0 | 0.11 | 2027 |
| 1 | –, aleurone | TLC | 56.2 | 12.6 (incl. PG) | | 16.8 | (LPC 3.8) | 1.7 | 2.3 | 0.16 | 2027 |
| 1 | –, nonstarchy endosperm | TLC | 6.5 | 11.4 (incl. PG) | | | | 3.2 | 2.6 | 0.05 | 2027 |
| | | | also LPC 35.1, LPE 0.8 | | | | | | | | |
| 1 | –, starchy endosperm | TLC | 0.6 | | | 1.0 | | 2.4 | | 0.63 | 2027 |
| | | | also LPC 82.5, LPE 7.9, LPG 4.1, LPI-LPS 1.5 | | | | | | | | |
| 2 | Leaf | TLC | | 21.9-24.9 | | | | | | 1.55-2.21 | 2032 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 23.9-33.0 | | | | | | | | |
| 2 | –, chloroplast[m] (1) | TLC | 0.08 | 0.20 | | | | | | | |
| | –, chloroplast (2) | TLC | 0.13 | 0.22 | | | | | | | 1437 |
| *Triticum macha* Dek. and Men. (Macha Wheat) | | | | | | | | | | | |
| 2 | Leaf, chloroplast[m] (1) | TLC | 0.05 | | 0.23 | | | | | | 1437 |
| | Leaf, chloroplast[m] (2) | TLC | 0.08 | | 0.20 | | | | | | |
| *Triticum monococcum* L. (Einkorn) | | | | | | | | | | | |
| 2 | Leaf, chloroplast[m] (1) | TLC | 0.10 | | 0.23 | | | | | | 1437 |
| | Leaf, chloroplast[m] (2) | TLC | 0.07 | | 0.24 | | | | | | |
| 1 | Cell culture | TLC | 50.7 | 35.9 | 3.3 | 6.0 | | 4.1 | | | 2041 |
| *Triticum spelta* L. (Spelt) | | | | | | | | | | | |
| 2 | Leaf, chloroplast[m] | TLC | 0.07-0.10 | | 0.22-0.28 | | | | | | 1437 |
| *Tulipa* spp. (Tulip) | | | | | | | | | | | |
| 1 | Leaf | TLC | | | 13 | | | | | | 1440 |
| 1 | Tuber | TLC | 37.1 | 44.2 | 2.6 | | | 7.0 | 8.9 | 0.178 | 1446 |
| *Tussilago farfara* L. (Coltsfoot) | | | | | | | | | | | |
| 1 | Leaf | TLC | 48.1 | 19.5 | 13.0 | 9.1 | 0 | 10.4 | | 1.54[x] | 2042 |
| *Typha latifolia* L. (Cattail) | | | | | | | | | | | |
| 1 | Pollen | TLC | + | + | + | + | | + | + | 4.5[c] | 2043 |
| 1 | Pollen | TLC | 63.2 | 18.3 | 7.0 | 7.8 (incl. PS) | | 1.0 | 2.7 | | 2044 |
| 1 | | TLC | 57.9 | 17.9 | 6.6 | 6.3 (incl. PS) | | 3.5 | 5.1 | | 2044 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Microsomal membrane | | also LPC 1.8, LPE 1.0 | | | | | | | | |
| *Urtica dioica* L. (Stinging Nettle) | | | | | | | | | | | |
| 1 | Leaf and stem | HPLC | + | + | | + | | | (LPC +) | | 2045 |
| 1 | Root | HPLC | + | + | | + | | | (LPC +) | | 2045 |
| *Utricularia vulgaris* L. (Bladderwort) | | | | | | | | | | | |
| 1 | whole plant | TLC | 47.4 | 20.4 | 11.0 | 9.0 | 3.4 | | 8.8 | 4.92[c] | 1555 |
| *Vaccinium macrocarpon* Ait. (Cranberry) | | | | | | | | | | | |
| 1 | Seed | TLC | 90 | 5 | | | 5 | | (LPC trace) | 0.26[c] | 2046 |
| *Vaccinium myrtillus* L. (Whortleberry) | | | | | | | | | | | |
| 1 | Fruit | | 0.086 | | | | | | | | 1527 |
| *Vallisneria gigantea* Graebn. (Eelgrass) | | | | | | | | | | | |
| 1 | Whole plant | TLC | 42.5 | 25.9 | 12.8 | 6.8 | 7.0 | | 5.2 | 5.11[c] | 1555 |
| *Vallisneria spiralis* L. | | | | | | | | | | | |
| 1 | Whole plant | TLC | 46.8 | 21.1 | 13.9 | 7.2 | 6.6 | | 6.1 | 4.82[c] | 1555 |
| *Vanda teres* (Roxb.) Lindl. | | | | | | | | | | | |
| 1 | Leaf[l] | TLC | | | 0.20 | | | | | | 1402 |
| *Vicia faba* L. (Broad (Faba) Bean) | | | | | | | | | | | |
| 1 | Seed | TLC | 40.2 | 43.1 | | 11.4 | 5.3 | | | 0.92 | 1872 |
| 1 | Bean | TLC | 50.3 | 16.4 | 3.1 | 15.6 | | | (NAPE 13.0) | 1.05 | 1693 |
| 1 | Starch | TLC | + | 0 | | | + | | (LPC +, LPE 0, LPS +) | | 1902 |
| 1 | Leaf | TLC | 31.9 | 15.3 | 25.8 | 7.9 | | | 19.1 | 0.46 | 2047 |
| 1 | Leaf protoplast | TLC | 31 | 17 | 52 | | | | | 29[d] | 2048 |
| 1 | –, guard cells | TLC | 52 | 23 | 9 | 10 | | 3 | 3 | | 2049 |
| 1 | –, mesophyll cells | TLC | 37 | 13 | 35 | 5 | | 1 | 9 | | 2049 |
| 1 | Leaf chloroplast envelope membrane | TLC | 77 | Trace | 22 | Trace | | | | | 2050 |
| 1 | –, lamella | TLC | 34 | Trace | 66 | Trace | | | | | 2050 |
| 1 | –, mitochondria | TLC | 57 | 33 | 10 | Trace | | | | | 2050 |
| 1 | –, microsomes | TLC | 67 | 20 | 13 | Trace | | | | | 2050 |
| 1 | Root | TLC | 44.5 | 30.7 | 6.7 | 7.9 | 4.0 | 3.7 | 2.5 | | 1775 |
| 1 | –, mitochondria *Incl. PS | TLC | 47.2 | 20.3 | 15.1* | 13.2 | | 1 | 3.2 | 83.4[a] | 1776 |
| 1 | | TLC | 42.1 | 26.6 | 13.6* | 10.4 | | 2.1 | 5.3 | 82.3[a] | 1776 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | –, microsomes | | | | | | | | | | |
| | *Incl. PS | | | | | | | | | | |
| *Vicia faba minor* L. | | | | | | | | | | | |
| 1 | Root | TLC | 44.5 | 30.7 | 6.7 | 7.9 | 4.0 | 3.7 | 2.5 | | 1775 |
| *Vicia villosa* Roth. (Hairy Vetch) | | | | | | | | | | | |
| 1 | Seed[c] | Frac. pptn. | 0.304 | 0.081 | | | | | | | 718 |
| *Vigna angularis* (Willd.) Ohwi and Ohashi (Adzuki Bean) | | | | | | | | | | | |
| 1 | Bean | TLC | 50.9 | 20.9 | 0.1 | 21.2 | | (NAPE 4.2) | | 1.10 | 1693 |
| 1 | Leaf | TLC | 32 | 24 | 36 | 4 | | <4 | (NAPE 4) | | 2051 |
| 1 | Root | TLC | 14 | 6 | <3 | 3 | | <1 | (NAPE 6) | | 2051 |
| 1 | Suspension culture, leaf | TLC | 23 | 23 | 1 | 7 | | (NAPE 4, BPA 7) | | 0.20 | 2052 |
| 1 | –, cotyledon | TLC | 22 | 22 | 1 | 5 | | (NAPE 4, BPA 11) | | 0.29 | 2052 |
| 1 | –, hypocotyl | TLC | 24 | 26 | 1 | 6 | | (NAPE 4, BPA 4) | | 0.26 | 2052 |
| 1 | –, root | TLC | 16 | 20 | 1 | 9 | | (NAPE 4, BPA 13) | | 0.13 | 2052 |
| *Vigna auriculata* (Ronji) | | | | | | | | | | | |
| 1 | Seed | TLC | 40.0 | 40.0 | | 19.7 | Trace | | | 1.38 | 1872 |
| *Vigna mungo* (L.) Hepper (Black Gram, Matpe) | | | | | | | | | | | |
| 1 | Seed | TLC | 34.6 | 30.0 | 0.5 | 21.4 | + | + | 2.1 | 1.01 | 1384 |
| | | | also NAPE 9.0, NALPE 0.8, LPC +, LPE + | | | | | | | | |
| *Vigna radiata* (L.) Wilcz. (Mung Bean) | | | | | | | | | | | |
| 1 | Seed | TLC | 37.0 | 31.5 | 3.6 | 24.4 | 1.8 | 0.4 | | | 2053 |
| 1 | Seed | TLC | 61.0 | 21.1 | | 10.8 | | 1.1[u] | | 1.4[c] | 2054 |
| | | | also NAPE 2.1, NALPE 1.9, LPC 1.0 | | | | | | | | |
| 1 | –, mitochondrial inner membrane | TLC | 33 | 32 | 4 | 5 | | (LPE 3) | 23 | | 2055 |
| 1 | Seed flour, free | TLC also LPC 2.8 | 10.8 | 64.7 | 0.5 | 5.3 (incl. PS) | | | 16.7 | 0.041 | 2056 |
| 1 | –, bound | TLC also LPC 1.8 | 20.5 | 35.2 | 0.8 | 26.7 (incl. PS) | | | 15.0 | 0.17 | 2056 |
| 1 | Hypocotyl, 3 days old | TLC | PC, PE, PI, and PA measured back along 5 mm segments from apex | | | | | | | | 2057 |
| 1 | –, plasma membrane | TLC | 32.7 | 38.0 | 4.5 | 5.3 | 3.1 | 16.3 | | 1.29[h] | 2058 |
| 1 | –, plasma membrane | HPLC | 23 | 53 | | 7 | | 17 | | 0.3-0.6[t] | 2059 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, tonoplast | TLC | 46.5 | 31.4 | 4.5 | 11.2 | 4.3 | 2.2 | | 1.93[h] | 2058 |
| 1 | –, mitochondria | TLC | 36 | 46 | 1 | 2.5 | | | 14 | 300[j] | 1432 |
| 1 | –, inner membrane | TLC | 29 | 50 | 1 | 2 | | | 17 | 380[j] | 1432 |
| 1 | –, outer membrane | TLC | 68 | 24 | 2 | 5 | | | 0 | 800[j] | 1432 |
| 1 | Leaf chloroplast | TLC | 59.0 | 0 | 28.5 | 11.5 | | | | 20.0[g] | 2060 |
| 1 | Seedling | TLC | 42 | 16 | 6 | 3 | | 16 | 10 (LPC 8) | 0.24 | 2061 |
| 1 | Seedling, 2 days old | TLC | 43.6 | 32.7 | 4.7 | 15.0 | 1.9 | 3.2 | | | 2053 |
| 1 | Seedling, 7 days old, axis | TLC | 40.9 | 39.5 | 3.1 | 11.4 | 1.0 | 4.1 | | | 2053 |
| 1 | –, cotyledon | TLC | 35.4 | 33.3 | 6.3 | 12.5 | 1.9 | 8.1 | | | 2053 |
| 1 | Root, plasma membrane | TLC | 29.2 | 12.7 | 2.1 | 6.1 (incl. PS) | | 10.5 | | | 2062 |
| *Vigna unguiculata* (L.) Walp. (Cowpea) | | | | | | | | | | | |
| 1 | Seed | TLC | 18 | 30 | 24 | 16 | | | 12 | 0.20[c] | 1524 |
| 1 | Leaf | TLC | 38.9 | 30.4 | 15.3 | 8.1 | | 7.4 | | | 2063 |
| 2 | Leaf | HPLC | 51-59 | | 19-20 | | | | | 1.20-1.69[a] | 2064 |
| 1 | Internode | TLC | 55.4 | 29.7 | | 10.3 | | 4.6 | | | 2063 |
| *Vinca minor* L. (Periwinkle) | | | | | | | | | | | |
| 1 | Leaf[a] | TLC | 13 | 5 | 10 | | | | | | 2065 |
| *Viscum album* L. (Mistletoe) | | | | | | | | | | | |
| 1 | Leaf chloroplast[y] | TLC | 158 | | + | + | | | | 20 | 2009 |
| *Vitis riparia* Michx. (Riverbank Grape) | | | | | | | | | | | |
| 1 | Root *Incl. PS | TLC | 42.1 | 35.8* | 9.0 | 2.8 | | 5.9 | 4.5 | | 1699 |
| *Vitis vinifera* L. (Wine Grape) | | | | | | | | | | | |
| 10 | Seed | TLC | 16.5-43.6 | 22.0-41.7 | | 15.3-28.4 | Trace | 11.8-17.6 | | 0.81-1.12[a] | 2066 |
| 1 | Leaf | TLC | 2.3 | 15.0 | 34.2 | 6.7 | 16.0 | | (LPE 7) | 1.81[c] | 2067 |
| 1 | –, chloroplast | TLC | 9.8 | 10.5 | 43.4 | 12.5 | 4.4 | | (LPE 0) | 2.94[c] | 2067 |
| 1 | Leaf, plasma membrane | HPLC | 60.0 | 40.0 | 0 | | | | 0 | 88.3[j] | 2068 |
| 1 | –, microsomes | HPLC | 20.5 | 15.7 | 2.9 | | | | 60.9 | 54.7[j] | 2068 |
| 1 | Seed | TLC | + | + | | + | | Trace | | 0.4 | 1777 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | also LPC +, LPI + | | | | | | | | |
| 1 | Berry | TLC | 29.7 | 32.3 | 10.9 | 5.6 | 8.4 | 3.6 | 4.3 | 0.058 | 2069 |
| | | | also LPC 2.2, LPE 3.0 | | | | | | | | |
| 1 | –, seed | TLC | 25.1 | 36.3 | 6.3 | 8.1 | 10.4 | 6.7 | 3.0 | 1.12 | 2069 |
| | | | also LPC 1.9, LPE 2.2 | | | | | | | | |
| 1 | –, skin | TLC | 27.6 | 34.0 | 10.4 | 6.1 | 8.8 | 3.5 | 2.4 | 0.038 | 2069 |
| | | | also LPC 3.2, LPE 4.0 | | | | | | | | |
| 1 | –, flesh | TLC | 31.2 | 27.4 | 12.3 | 4.0 | 7.6 | 2.2 | 9.2 | 0.012 | 2069 |
| | | | also LPC 2.7, LPE 3.4 | | | | | | | | |
| 1 | Root<br>*Incl. PS | TLC | 47.6 | 34.7* | 4.9 | 1.4 | | 5.0 | | | 1699 |
| 5 | Root | CC (silica) | 34.5-68.2 | 31.8-65.5 | | Trace | | | | 0.024-0.084 | 2070 |
| *Withania somnifera* (L.) Dun. (Winter Cherry, Aswagandh) | | | | | | | | | | | |
| 1 | Seed | TLC | 34.0 | 22.4 | | 24.8 | | | 17.8 | 0.70[c] | 1757 |
| | | | also LPC 0.7, LPE 0.5 | | | | | | | | |
| *Xanthium orientale* L. (Oriental Cocklebur) | | | | | | | | | | | |
| 1 | Leaf | TLC | 50 | 15 | 25 | 5 | | | 4 | 0.99[l] | 1523 |
| *Xanthium strumarium* L. (Cocklebur) | | | | | | | | | | | |
| 1 | Young fruit | Frac. pptn. | 33.2 | 66.8 | | | | | | 0.18 | 2071 |
| *Zantedeschia aethiopica* (L.) Spreng. (Calla Lily) | | | | | | | | | | | |
| 1 | Leaf thylakoid[m] | TLC | 0.131 | | 0.191 | | | | | | 2072 |
| 1 | Regreened spathe, thylakoid[m] | TLC | 0.215 | | 0.240 | | | | | | 2072 |
| *Zea mays* L. (Corn, Maize) | | | | | | | | | | | |
| 10 | Seed[cc] | TLC | + | | | | | | | 0.065-0.233 | 2073 |
| 1 | –, germ | TLC | 54.5 | 11.7 | 4.3 | 18.7 | 0.9 | 1.2 | 2.1 | 2.54[c] | 1390 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/cm$^2$ leaf area; [y]Molecules per $10^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | also NAPE 1.1, NALPE 1.8, LPC 0.8, LPE 0.4 | | | | | | | | |
| 3 | –, germ[f] | TLC | 22.9-397 | 376-748 | 49-194 | 19-36 | 59-333 | | | 1224-1453[c] | 2074 |
| | | | also NAPE 73-117, LPC 9-60, LPE 11-18, LPI, 0.28 | | | | | | | | |
| 1 | –, chloroplast envelope membrane[a,c] | TLC | 6.7 | 1.1 | 2.2 | 1.4 | | | 0.8 | 11.4 | 1728 |
| 3 | –, pericarp[f] | TLC | 2-7 | 5-8 | 1-4 | 2-4 | | 2-7 | | 27-42[c] | 2074 |
| | | | also NAPE 5-11, LPC 3-7, LPE 1-3 | | | | | | | | |
| 3 | –, tip cap[f] | TLC | 15-32 | 7-41 | 3-27 | 3-8 | | 14-24 | | 52-185[c] | 2074 |
| | | | also NAPE 10-15, LPC 10-28, LPE 0-3, LPI 0.18 | | | | | | | | |
| 1 | –, endosperm | TLC | 44.6 | 6.1 | 1.9 | 3.6 | 0 | 0.7 | 0.9 | 0.52[c] | 1390 |
| | | | also NAPE 1.2, NALPE 1.1, LPC 35.1, LPE 3.4 | | | | | | | | |
| 3 | –, nonstarch endosperm[f] | TLC | 1-31 | 1-8 | Trace-6 | 3-9 | | Trace-12 | | 5-101[c] | 2074 |
| | | | also NAPE trace-3, LPC 1-29, LPE 0-4 | | | | | | | | |
| 1 | –, amyloplast envelope | TLC | 37.3 | 4.5 | 19.4 | 23.9 | | | (LPC 4.5) | | 2075 |
| 1 | Seed, oil body | TLC | 64.1 | 8.1 | | 7.6 | 20.2 | | | 0.91 | 1482 |
| 1 | Seed, oil body | TLC | | | | | 0 | | | | 1571 |
| 1 | –, stele[j] | HPLC | 88.9 | 42.4 | | + | + | + | | | 2076 |
| 1 | –, cortex[j] | HPLC | 59.0 | 45.9 | | + | + | + | | | 2076 |
| 1 | Seed starch, waxy | TLC | | | | | | | (LPC 0) | 0.23[d] | 2077 |
| 1 | –, nonwaxy | TLC | | | | | | | (LPC 17) | 0.87[d] | 2077 |
| 1 | –, amylomaize | TLC | | | | | | | (LPC 19) | 1.11[d] | 2077 |
| 1 | Leaf | TLC | 28 | 11 | 44 | 17 | | | | | 1842 |
| 1 | Leaf | TLC | 15 | 28 | 22 | | | | 18 | 1.42[l] | 1698 |
| 1 | Leaf | TLC | | | | | + | | | | 1450 |
| 1 | Leaf chloroplast | TLC | 41.1 | 0 | 31.4 | 22.3 | | | | 28.7[g] | 2060 |
| 1 | –, bundle sheath[a] | TLC | | | 9 | | | | | | 1489 |
| 1 | –, agranal[a] | TLC | 7 | | 12 | | | | | | 2078 |
| 1 | –, mesophyll[a] | TLC | | | 9 | | | | | | 1489 |
| 1 | Leaf thylakoid | | | | | | | | | | |
| 1 | –, granum[a] | TLC | 4 | | 14 | | | | | | 2078 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, stroma[a] | TLC | 6 | | 12 | | | | | | 2078 |
| 1 | Leaf starch | TLC | | | | | | LPC 0, LPE +, LPS 0 | | | 1902 |
| 1 | Seedling coleoptile, microsome | TLC | | | | PI[H] | | | | | 2079 |
| 1 | –, plasma membrane | TLC | | | | PI[H] | | | | | 2079 |
| 1 | Anther wall | TLC | 43 | 31 | 6 | 20 | | | | | 1842 |
| 1 | Pollen grain | TLC | 55.3 | 30.0 | 1.8 | 9.5 (incl. PS) | | 2.2 | 1.3 | 6.09[c] | 1861 |
| 1 | Root<br>*Incl. PS | TLC | 51.2 | 36.1* | 5.7 | Trace | | 3.3 | 3.5 | | 1699 |
| 1 | Root, 6 days old | TLC | 45.6 | 24.2 | 6.8 | | 11.5 | 3.4 | 6.0 | 0.88 | 1583 |
| 1 | Root[a] | HPLC | 30.2 | 15.9 | Trace | Trace | 0 | 13.5 | 0.3 | | 1413 |
| 1 | –, endoplastic reticulum | TLC | 54 | 24 | 8 | 10 (incl. PS) | | 3 | | 0.98[j] | 2080 |
| 1 | –, mitochondria | TLC | 34 | 30 | 10 | 7 (incl. PS) | | 20 | | 0.33[j] | 2080 |
| 2 | Root plasma membrane | TLC | 47.1-62.2 | 21.4-23.4 | 4.9-10.5 | 8.4-8.9 | 0-1.5 | 1.6-9.2 | 0 (LPC 0-0.9) | 668[f] | 2081 |
| 1 | Seedling, root | TLC | 48.4 | 25.3 | | | 8.4 | | | 25.3[k] | 2082 |
| 1 | Cell suspension culture | $^{31}$P NMR | + | + | | | + | | | | 2083 |
| *Zea mays* L. ssp. *indentata* (Sturt.) Bailey (Dent Corn) | | | | | | | | | | | |
| 6 | Seed | TLC | 4.5-22.0 | | | 30.9-86.4 | | | | 0.10-0.31 | 2084 |
| *Zea mays* L. ssp. *indurata* (Sturt.) Bailey (Flint Corn) | | | | | | | | | | | |
| | Seed | TLC | 27.2-29.5 | | | 42.9-79.1 | + | | + | | 2085 |
| *Zea mays* L. ssp. *saccharata* Sturt. (Sweet Corn) | | | | | | | | | | | |
| 1 | Seed | TLC | 65 | 16 | | 12 | | | (LPC +, LPE +) | | 2086 |
| *Zingiber officinale* Rosc. (Ginger) | | | | | | | | | | | |
| 14 | Rhizome | TLC | + | | | + | | + | (LPC +) | | 2087 |
| *Ziziphus jujuba* Mill. (Jujube) | | | | | | | | | | | |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percent by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL; [a]Percent of total lipids; [b]mg lipid P/100 mL juice; [c]Percent dwb; [d]mg PL/100 mg protein; [e]mg PL/g fwb; [f]mg PL/100 g dwb; [g]Percent of polar lipids; [h]μmol PL/mg protein; [i]μmol PL/mg chlorophyll; [j]μg PL/mg protein; [k]μg lipid P/g; [l]μmol PL/g fwb; [m]mol PL/mol chlorophyll; [n]mg PL/g dwb; [o]μmol PL/g dwb; [p]μg PL/100 mg fwb; [q]μg PL/mg chlorophyll; [r]mg PL/cm$^2$ leaf area; [s]nmol PL/cm$^2$ leaf area; [t]μmol PL/mg protein; [u]IR given; [v]mg lipid P/g lipid; [w]μg PL/mL; [x]μg lipid P/cm$^2$ leaf area; [y]Molecules per 10$^6$ plastids; [z]μg PL/mg chromatin; [aa]Fatty acid composition and *sn*-1/*sn*-2 distribution given for each phospholipid; [bb]μg/g fwb; [cc]Taken from the abstract.

*Continued*

**Table 4-15** Phospholipids in Plants*—cont'd

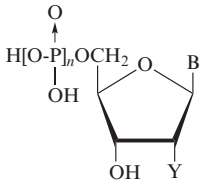
| No. | Plant part | Method | PC | PE | PG | PI | PS | PA | DPG | PL | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Seed | TLC | 42.3 | 8.4 | 11.5 | 11.1 | | 7.2 | | 0.17[c] | 2088 |
| | | | also NAPE 7.4, NALPE 3.8, LPC 4.1, LPE 1.9, LPI 2.3 | | | | | | | | |
| 1 | –, pericarp | TLC | 18.8 | 9.8 | 28.1 | 17.5 | | 7.1 | | 0.05[c] | 2088 |
| | | | also NAPE 8.6, NALPE 0, LPC 3.7, LPE 0, LPI 0 | | | | | | | | |
| *Zostera asiatica* Miki | | | | | | | | | | | |
| 1 | Whole plant (NAPE trace) | TLC | 43.8 | 23.8 | 14.6 | 12.6 | 2.2 | Trace | 3.0 | 0.14 | 1882 |
| *Zostera capricorni* Asch. | | | | | | | | | | | |
| 1 | Seed | HPLC | 4 | 21 | | 74 | | | | 0.56[c] | 2089 |
| *Zostera marina* L (Seawrack) | | | | | | | | | | | |
| 1 | Whole plant (NAPE trace) | TLC | 41.8 | 24.3 | 15.8 | 12.1 | 2.6 | Trace | 3.4 | 0.11 | 1882 |
| *Zostera nana* Roth | | | | | | | | | | | |
| 1 | Whole plant | TLC | 45.1 | 24.3 | 15.5 | 10.3 | 4.8 | | | 0.11[c] | 2090 |
| *Zygophyllum album* L.f. (White Bean Caper) | | | | | | | | | | | |
| 1 | Shoot | TLC | 29.6 | 16.9 | 10.0 | 5.3 | | 9.0 | 21.7 | 0.189[c] | 1488 |

*Unless stated otherwise; the PL column gives the total phospholipid content of each plant part in percentage by weight, and the PC, PE, PG, PI, PS, PA, and DPG columns show the distribution in percent by weight of the total PL.

[a]Percentage of total lipids.
[b]mg lipid P/100 mL juice.
[c]Percentage of dwb.
[d]mg PL/100 mg protein.
[e]mg PL/g fwb.
[f]mg PL/100 g dwb.
[g]Percentage of polar lipids.
[h]μmol PL/mg protein.
[i]μmol PL/mg chlorophyll.
[j]μg PL/mg protein.
[k]μg lipid P/g.
[l]μmol PL/g fwb.
[m]mol PL/mol chlorophyll.
[n]mg PL/g dwb.
[o]μmol PL/g dwb.
[p]μg PL/100 mg fwb.
[q]μg PL/mg chlorophyll.
[r]mg PL/$cm^2$ leaf area.
[s]nmol PL/$cm^2$ leaf area.
[t]μmol PL/mg protein.
[u]IR given.
[v]mg lipid P/g lipid.
[w]μg PL/mL.

# 5 Mononucleotides

This group comprises the mono-, di-, and triphosphate derivatives of the ribo- and deoxyribonucleosides of the purine bases adenine and guanine and the pyrimidine bases cytosine, uracil, and thymine. The following is a complete list of the compounds discussed in this chapter, except for the cyclic nucleotides and sugar nucleotides which are discussed later in the chapter:




B = A, G, C, U or T
Y = OH or H
*n* = 1, 2, or 3

| B | Base | Nucleoside | Nucleotide |
|---|---|---|---|
| *Ribose derivatives, Y = OH* | | | |
| A | Adenine | Adenosine | AMP, ADP, ATP |
| G | Guanine | Guanosine | GMP, GDP, GTP |
| C | Cytosine | Cytidine | CMP, CDP, CTP |
| U | Uracil | Uridine | UMP, UDP, UTP |
| *Deoxyribose derivatives, Y = H* | | | |
| A | Adenine | Adenosine | dAMP, dADP, dATP |
| G | Guanine | Guanosine | dGMP, dGDP, dGTP |
| C | Cytosine | Cytidine | dCMP, dCDP, dCTP |
| U | Uracil | Uridine | dUMP, dUDP, dUTP |
| T | Thymine | Thymidine | TMP, TDP, TTP[a] |

[a]Often designated dTMP, dTDP, and dTTP in the literature despite the fact that thymidine already has the 2′-deoxyribose structure.

For general references on this subject, see Feingold,[2426] Pradet and Raymond,[2427] Wasternack,[2428] Brown,[2429] or Townsend.[2430]

## Occurrence

Although the structures and properties of the ribonucleotides which comprise the building blocks of ribonucleic acid (RNA) have been known for some time, the occurrence of free nucleotides in higher plants was not established until the mid-1950s. The first nucleotides to be discovered in the free state were ADP and ATP, isolated from mung bean seedlings by Albaum *et al.* in 1950 and shown to be similar if not identical to those found in animal tissues.[2431] The application of ion-exchange chromatography (IEC) in 1956 to separate the acid-soluble ribonucleotides from each other enabled Bergkvist[2432] and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Ginsburg *et al.*[2433] to identify AMP, ADP, ATP, GMP, GDP, GTP, CTP, UMP, UDP, and UTP in wheat and mung beans, respectively. By 1960 all 12 of the ribonucleotide mono-, di-, and triphosphates had been isolated and quantitated. Over the succeeding years, the number of papers devoted to this subject has expanded rapidly, as attested to in the tables that accompany this chapter.

In contrast, very little is known about the occurrence in the free state of the deoxyribonucleotides which comprise the building blocks of deoxyribonucleic acid (DNA). The triphosphates dATP, dGTP, dCTP, and TTP were identified in pine pollen and in sycamore and tobacco callus culture[2434] and the corresponding diphosphates dADP, dGDP, dCDP, and TDP in tomato root tips.[2435] The monophosphates dAMP, dGMP, dCMP, and TMP have yet to be detected in the higher plants.

The metabolic pathways for the biosynthesis of the nucleotides are outlined in Figs. 5-1 and 5-2. The key precursor for the purine nucleotides is inosinic acid (IMP), which is formed from α-D-ribose 5-phosphate (R5P) by a sequence of reactions whose final step is closure of the purine ring. AMP is formed from IMP by ammonolysis of the hydroxyl group at C-6 (Fig. 5-1, step 1), whereas GMP is formed by the introduction of an amino group at C-2 (step 8). Stepwise reversible phosphorylation of AMP or GMP yields ADP, ATP, GDP, and GTP (steps 5-7). Enzymatic reduction of ADP or GDP (step 9) provides the point of entry to the deoxyribonucleotides dADP and dGDP, from which dATP, dGTP, dAMP, and dGMP are formed by reversible phosphorylation (steps 5-7). Steps 2-4 provide a mechanism for purine salvage from AMP, GMP, dAMP, and dGMP. The purine nucleotides needed for the biosynthesis of RNA are furnished by ATP and GTP while those needed for the biosynthesis of DNA are furnished by dATP and dGTP.

The key precursor for the pyrimidine nucleotides is orotidine 5′-phosphate (OMP), which is formed from 5′-phosphoribose-1-pyrophosphate (PRPP) by condensation with

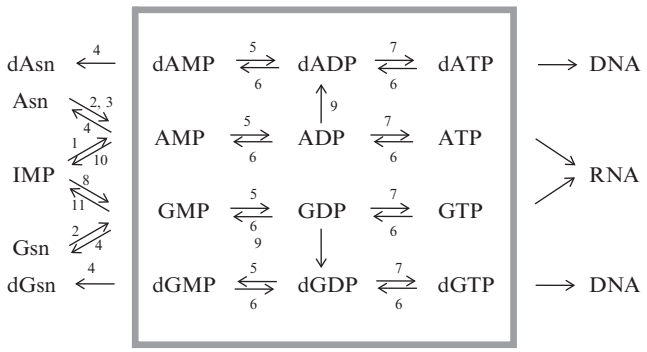



**FIGURE 5-1 Purine Nucleotides.** (1) Adenylosuccinate synthetase [E.C. 6.3.4.4], aspartate, Mg(II); adenylosuccinate lyase [E.C. 4.3.2.2]. (2) Nucleoside phosphotransferase [E.C. 2.7.1.77]. (3) Adenylate kinase [E.C. 2.7.1.20]. (4) 5′-Nucleotidase [E.C. 3.1.3.5]. (5) Nucleoside monophosphate kinase [E.C. 2.7.4.4]. (6) Nucleoside diphosphatase [E.C. 3.6.1.6]. (7) Nucleoside diphosphate kinase [E.C. 2.7.4.6]. (8) IMP dehydrogenase [E.C. 1.2.1.14], NAD, GMP synthetase [E.C. 6.3.4.1], glutamine. (9) Ribonucleoside diphosphate reductase [E.C. 1.17.4.1], NADPH, Mg(II), thioredoxin. (10) AMP aminohydrolase [E.C. 3.4.5.6]. (11) GMP reductase [E.C. 1.6.6.8].

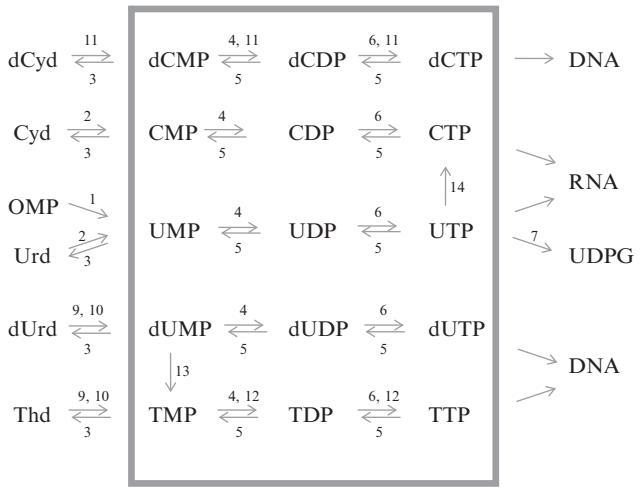



**FIGURE 5-2 Pyrimidine Nucleotides.** (1) Orotidine 5′-phosphate decarboxylase [E.C. 4.1.1.-23]. (2) Nucleoside phosphotransferase [E.C. 2.7.1.77]. (3) 5′-Nucleotidase [E.C. 3.1.3.5]. (4) Nucleoside monophosphate kinase [E.C. 2.7.4.4]. (5) Nucleoside diphosphatase [E.C. 3.6.1.6]. (6) Nucleoside diphosphate kinase [E.C. 2.7.4.6]. (7) Glucose 1-phosphate uridyltransferase [E.C. 2.7.7.9]. (8) Ribonucleoside diphosphate reductase [E.C. 1.17.4.1], NADPH, Mg(II), thioredoxin. (9) Thymidine kinase [E.C. 2.7.1.75]. (10) Thymidine AMP-phosphotransferase [E.C. 2.7.1.77]. (11) dCMP kinase [E.C. 2.7.4.14]. (12) TMP kinase [E.C. 2.7.4.9]. (13) Thymidylate synthetase [E.C. 2.1.1.6]. (14) CTP synthetase [E.C. 6.3.4.2], $NH_3$, Mg(II).

orotic acid. Decarboxylation of OMP yields UMP (Fig. 5-2, step 1), from which UDP and UTP are formed by stepwise reversible phosphorylation (steps 4 and 5). CTP is formed from UTP by ammonolysis of the hydroxyl group at C-4 (step 15) and dUDP is formed from UDP by enzymatic reduction (step 8).

## Extraction

Many plant tissues contain phosphatases which, if not destroyed or inactivated, are capable of hydrolyzing nucleotides during isolation. The extraction procedures most widely used in current practice employ ice-cold aqueous trichloroacetic acid (TCA) or perchloric acid (PCA), both of which kill the plant tissue and extract the nucleotides without degrading them. After extraction, the excess TCA is removed by extraction with ether and the excess PCA by precipitation as the water-insoluble potassium perchlorate. More concentrated acid should be avoided because it begins to solubilize nucleic acids such as RNA.[2436]

> *Pea seeds were milled in a Glen Creston C580 microhammer mill. . ., a screen of 0.1 mm. diameter mesh being used. The milled seed (10 g. samples) was homogenized in a MSE homogenizer for 3 min. at 0° with 0.3N-perchloric acid (25-30 ml) and the homogenate filtered under vacuum through a sintered-glass Buchner funnel (porosity 3) into a flask surrounded by crushed ice. Extraction from the almost dry residue was assisted by pressing with an inverted wide-topped glass stopper. The*

*homogenizer flask was rinsed out with four successive 10 ml. portions of 0.15N-perchloric acid and these washings were used to effect four further extractions of the seed residue in the funnel. The clear filtrate was adjusted to pH 7.2 with 20% (v/v) potassium hydroxide solution and, after standing at 0° for 45 min., was centrifuged to remove potassium perchlorate.*

Reproduced with permission from Brown, E. G., "The Acid-Soluble Nucleotides of Mature Pea Seeds", *Biochem. J.* **1962**, *85*(3), 633–640,[2437] © 1962 the Biochemical Society.

Bieleski[10] recommended the use of an ice-cold ternary mixture of methanol, chloroform and 1*M* formic acid (12:5:3) as the extractant, whereby any chlorophyll or terpenoid coextracted with the nucleotides are removed in the organic phase. Extraction with boiling 80% ethanol[6] is discouraged because it does not completely inactivate the phosphatases.[10]

The presence of phenolics in such plant extracts interferes with the direct determination of the nucleotide content by UV spectrophotometry. They cannot be separated satisfactorily from the nucleotides by differential extraction, solvent partitioning, gel filtration, ion-exchange chromatography, or sorption,[2438] but they can be removed by passing the extract through a column of polyvinylpyrrolidone (PVP), either alone[2439] or in combination with Amberlite-XAD-2,[2438] or by passing the extract through a disposable cartridge of phenylsilane-bonded silica gel[2440] or Cu(II)-loaded Chelex 100.[2441] Alternatively, the nucleotides themselves may be separated from the extracts by adsorption on charcoal, washing the charcoal to remove the contaminants, and then recovering the nucleotides:

*The extract was adjusted to within the range pH 3.5-4.0 with acetic acid and passed slowly through a column, 1.2 cm. diameter, containing a mixture of acid-washed Norit OL charcoal (500 mg.) and Hyflo Supercel (800 mg.) supported on a 2 mm.-thick bed of Hyflo Supercel on a sintered-glass disk (porosity 3). The column was washed with 20 ml. of water and eluted with 15 ml. of 25% (v/v) ethanol containing 0.5% (v/v) of aq. ammonia (sp. gr. 0.88). The charcoal mixture was not allowed to dry out at any stage of the procedure. Percolation of solutions through the column was facilitated by application of a positive air pressure of 1-2 lb./in$^2$.*

Reproduced with permission from Brown, E. G., "The Acid-Soluble Nucleotides of Mature Pea Seeds", *Biochem. J.* **1962**, *85*(3), 633–640,[2437] © 1962 the Biochemical Society.

For a critical survey of the methods for purifying plant extracts, see Brown.[2429]

## Separation and Analysis

### *(1) Paper Chromatography (PC) Method*

In the 1950s and 1960s, two-dimensional PC was the method of choice for the separation of plant nucleotides. The procedures are similar to those used for the sugar phosphates (Chapter 1, pp 2 and 3). Adequate resolution is achieved with the ternary solvents listed in Table 5-2 (Chapter 1) provided that precautions are taken to remove cations such as calcium, magnesium, or iron by the use of acid-washed paper,[2764] by treatment of the

**Table 5-1** Travel Constants of the Ribonucleotides

| Compound | PC ($R_f$)[a] 1st | PC ($R_f$)[a] 2nd | PE ($M_P$)[a] | TLC ($R_f$)[b] 1st | TLC ($R_f$)[b] 2nd | TLE ($M_{AMP}$)[c] |
|---|---|---|---|---|---|---|
| $P_i$ | 100 | 100 | 100 | 100 | 100 | |
| AMP | 130 | 55 | 19 | 142 | 95 | 100 |
| GMP | 59 | 43 | 47 | | | |
| CMP | 106 | 53 | 9 | | | |
| UMP | 87 | 62 | 60 | 92 | 86 | 139 |
| ADP | 94 | 27 | 63 | 122 | 52 | 178 |
| GDP | 44 | 23 | 85 | | | |
| CDP | 81 | 27 | 59 | | | |
| UDP | 65 | 28 | 103 | 73 | 51 | 222 |
| ATP | 70 | 14 | 93 | 105 | 45 | 219 |
| GTP | 35 | 12 | 107 | | | |
| CTP | 61 | 14 | 92 | 86 | 36 | |
| UTP | 50 | 15 | 127 | | | 252 |
| ADPG | | | | 113 | 49 | 151 |
| UDPG | 111[d] | 14[d] | 88 | 68 | 42 | 185 |

[a]Bieleski and Young.[9]
[b]Feige *et al.*[33]
[c]Jenner.[2723]
[d]Slight decomposition. Solvents (refer to list in Chapter 1, p 2): PC: B2 and A2; PE, 0.025*M* sodium butyrate buffer; TLC: N3 and A3.

plant extract with an ion-exchange resin,[9] or by the addition of EDTA to the solvent.[28,29] Of the ternary solvents listed, those used most often are B2 and N2 for the first dimension and A2 and N3 for the second dimension, but many variations of these and other ternary solvents are documented in the literature cited in Table 5-2. The $R_f$ values in solvents A2 and B2 for the nucleotides covered in this chapter are given in Table 5-1. Inspection of the data reveals that the mobility of each and every nucleotide decreases with increasing number of phosphate groups, i.e., NMP > NDP > NTP.

### *(2) Thin-Layer Chromatography (TLC) Method*

Bieleski[36] showed that the nucleotides could be separated by two-dimensional TLC in a fifth the time required for PC with no loss of resolution and a 20-fold increase in sensitivity. In most of the cases cited in Table 5-1, the TLC was performed using plates coated with 250-μ-thick layers of Macherey-Nagel unbound cellulose powder using the same solvents as those used for PC. The relative positions of the nucleotides and the patterns obtained by the two methods are almost identical. PEI-impregnated cellulose TLC plates were employed by Nygaard *et al.*[2434,2537,2669] and others.[2704] Silica gel gives inferior results[36] but is adequate for the separation of ATP from the other components of sieve-tube sap.[2693]

### *(3) Electrophoretic Methods*

The nucleotides can also be separated from each other by paper electrophoresis (PE)[9,32] or thin-layer electrophoresis (TLE).[309] These methods are most useful when coupled with PC

or TLC, particularly in view of the fact that the order of mobility is reversed. Inspection of the PE data in Table 5-1 reveals that the $R_f$ value of each nucleotide increases with increasing number of phosphate groups (i.e., NMP < NDP < NTP). The TLE values (not shown) follow the same trends.[309] In Bieleski's procedure, electrophoretic separations are carried out at pH 3.6 with 0.25*M* acetate buffer and 600 V for PE[9] or 0.28*M* acetate buffer and 1000 V for TLE.[36] Others have used citrate buffer[12,2723] or butyrate buffer[2578] at pHs ranging from 3.5 to 4.8 and voltages ranging from 300 V[2682] to 1400 V.[331]

*(4) Ion Exchange Chromatography (IEC) Method*

The use of IEC to separate the acid-soluble nucleotides of plants was introduced in 1956 by Bergkvist,[2432] who used a Dowex 1-X10 (formate) anion exchange column and gradient elution with formic acid/sodium formate. The procedures most often employed are convex[2765] or concave[2766] gradient elution with ammonium formate buffers at pH ~ 5, which separate the nucleotides in the order NMP > NDP > NTP and in the order C > U > A > G. Gradient elution with formic acid/ammonium formate at pH ~ 2 changes the latter to C > A > G > U but not the former.[2765] IEC resins of a lower degree of crosslinking are often used such as Dowex 1-X8,[2437] Dowex 1-X4,[2767] or Dowex 1-X2,[2768] and occasionally different kinds of supports such as DEAE-Sephadex A-25[2654] or PEI-cellulose.[2754] Other eluants have been employed such as HCl/NaCl,[2433] HCl/LiCl,[2689] HCl/$CaCl_2$,[2650] or $NH_4Cl$/borate.[442] The IEC method has been automated[2769] and adapted for large (kilogram) scale use.[2770]

*(5) High-Performance Liquid Chromatography (HPLC) Method*

This method, introduced in 1972,[2486] has largely supplanted the foregoing methods because of its vastly improved resolution, despite the highly sophisticated equipment required for its use. The HPLC method is usually performed in the IEC mode with strongly anionic supports similar to those used in IEC, but in some cases better separations are achieved with HPLC in the reversed phase mode or the ion-pairing mode. The following procedure is typical of HPLC in the ion-exchange mode:

> *The HPLC equipment (Waters, Milford, MA, U.S.A.) consisted of two Model 510 pumps, a Model 680 automated gradient controller, a U6K injector and a Model 481 LC spectrophotometer. Nucleotides were detected by monitoring the column effluent at 254 nm with sensitivity fixed at 1V a.u.f.s. Separations were performed on a Waters Radial Pak Partisil SAX10 cartridge (10 cm × 0.8 cm I.D.) using a Waters radial compression Z-module system. The elution buffer system used consisted of eluent A, 7mM ammonium dihydrogenphosphate (pH 3.8), and eluent B, 250 mM ammonium dihydrogenphosphate (pH 4.5) with 500 mM potassium chloride. Nucleotide samples (100 μl), obtained from plant root tips, were injected into the column. A linear gradient of eluant A to eluant B was applied for 20 min., followed by an isocratic period of 10 min with eluent B . . . . The flow-rate was maintained at 4 ml/min; analyses were performed at ambient temperature. Peaks were integrated . . . on a*

*Waters 740 data module. Individual components of the acid-soluble nucleotide pools were identified, using retention time relative to known standards and by injecting known internal standards.*

Dutta, I; O'Donovan, G. A.; Smith, D. W., "Nucleotide Extraction and Quantitation from Tomato Roots by High-Performance Liquid Chromatography", *J. Chromatogr.* **1988**, *444A*, 183–189,[2618] reprinted by permission of Elsevier, © 1988.

Some nucleotides that are not well resolved by anion exchange HPLC, such as AMP, ADP, and the dinucleotides NAD and NADP, can be separated by reversed phase HPLC using a column packed with Hypersil ODS or LiChrosorb RP18 and gradient elution with 0.2*M* $(NH_4)$-$H_2PO_4$ and acetonitrile.[2440] The nucleotides can also be separated by reversed phase HPLC under ion-pairing conditions, substituting tetrabutylammonium hydroxide for acetonitrile as the second component of the gradient.[2623] A further refinement of the latter procedure was derivatization of the nucleotides with chloroacetaldehyde and detection of the etheno derivatives of AMP, ADP, and ATP by fluorescence in order to eliminate any interference by the cytidine derivatives.[2455]

## Analysis Without Separation

### *(1) $^{31}P$ Nuclear Magnetic Resonance (NMR) Method*

This method provides a nondestructive means for examining the nucleotides in their natural environment. It is particularly suited for examining the behavior of the nucleotide di- and triphosphates (including sugar derivatives such as UDPG) because the large differences in chemical shift between the phosphorus atoms of each compound makes them easy to distinguish from other phosphorus-containing compounds that are known to be present, such as $G_6P$, $P_i$, or NAD. The resolution, however, is insufficient to distinguish one di- or triphosphate from another; the compounds identified by their authors as ADP, ATP, etc., in Table 5-2 do not necessarily contain adenosine exclusively. The method was originally (1983) applied to tobacco cell cultures[2629] and to maize root tips[544] that were placed in 10 mm NMR tubes under constant aeration and scanned without spinning. In both cases the di- and triphosphates were found to be complexed to Mg(II) and to be present in a cytoplasmic (pH ~ 7.1) rather than a vacuolar (pH ~ 5.5) environment. $^{31}P$ NMR relaxation measurements showed that 30% of the NTP in maize root tips was also protein-bound.[2771] The method has since been applied to cell suspensions[51,2507,2695] and root tips[44,526,542,543,2589,2771] of other plants, soybean root nodule,[2563] potato tuber mitochondria,[2708] Jerusalem artichoke stolon,[45] lettuce[48] and fiddleneck[2644] sprouts, rice and wheat shoots,[2638] sunflower stem,[2563] spinach leaf and chloroplast,[50] avocado fruit,[515] and tobacco pollen.[2563] Use of the maximum entropy method (MEM) instead of fast Fourier transform (FFT) results in resolution comparable to that obtained with extracts (next paragraph), but so far this technique has only been applied to mung bean tips.[543]

As might be expected, better resolution in obtained with perchloric acid extracts of plant tissues than with living plant tissues, and other signals can now be identified. Using a multinuclear probe at 162.0 MHz, Bligny *et al.*[50] were able to identify AMP, ADP, ATP,

**Table 5-2** Ribonucleotides in Plants*

| No. | Plant part | Method | AMP | ADP | ATP | GMP | GDP | GTP | CMP | CDP | CTP | UMP | UDP | UTP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Abies procera* Rehd. (Noble Fir) | | | | | | | | | | | | | | | |
| 1 | Pollen | Lumin. | | | 20-530 | | | | | | | | | | 2442 |
| *Acer mono* Max. (Gorose) | | | | | | | | | | | | | | | |
| 1 | Sap[a] | | + | | | + | | | + | | | + | | | 2443 |
| *Acer opalus* Mill. (Italian Maple) | | | | | | | | | | | | | | | |
| 1 | Phloem exudate[b] | Enzym. | | | 250 | | | | | | | | | | 2444 |
| *Acer platanoides* L. (Norway Maple) | | | | | | | | | | | | | | | |
| 1 | Seed, cotyledon[c] | Lumin. | | | 5.71 | | | | | | | | | | 2445 |
| 1 | –, embryonic axis[c] | Lumin. | | | 1.58 | | | | | | | | | | 2445 |
| *Acer pseudoplatanus* L. (Sycamore Maple) | | | | | | | | | | | | | | | |
| 1 | Leaf bud[b] | Lumin. | 10 | 5 | 1 | | | | | | | | | | 2446 |
| 1 | Callus tissue[b] | TLC/TLC | | | 680 | | | 110 | | | 50 | | | 130 | 2434 |
| 1 | Cell suspension culture[b] | IEC | 90 | 136 | 570 | 260 | | 64 | 6 | | | 304 | | 44 | 2447 |
| 1 | Cell suspension culture | Lumin. | | | 280 | 1260 | | | | | | | | | 2448 |
| 1 | –, extract | $^{31}$P NMR | | | NMP, NDP, NTP, N = mainly A and U | | | | | | | | | | 51 |
| 1 | –, *in vivo* | $^{31}$P NMR | | | NDP, NTP, N = mainly A and U | | | | | | | | | | 51 |
| 1 | Cell suspension culture[f] | Enzym. | 6 | 37 | 62 | | | | | | | | | | 2449 |
| *Acer pseudosieboldianum* (Pax) Kom. (Korean Maple) | | | | | | | | | | | | | | | |
| 1 | Sap | | + | | | + | | | + | | | + | | | 2443 |
| *Acer saccharum* Marsh. (Sugar Maple) | | | | | | | | | | | | | | | |
| 1 | Embryonic axis[d] | Lumin. | 690.8 | 180.2 | 46.9 | | | | | | | | | | 2450 |
| *Actinidia arguta* (Sieb. and Zucc.) Planch. ex Miq. (Tara Vine) | | | | | | | | | | | | | | | |
| 1 | Sap[a] | – | + | | | + | | | + | | | + | | | 2451 |
| *Actinidia chinensis* Planch. ssp. *hispida* G.F. Liang | | | | | | | | | | | | | | | |
| 1 | Seed[a] | | | | + | | | | | | | | | | 2452 |
| *Actinidia deliciosa* Liang and Ferg. (Kiwi) | | | | | | | | | | | | | | | |
| 1 | Fruit | Enzym. | | 14.6 | 33.6 | | | | | | | | | | 222 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Agropyron desertorum* (Link.) Beauv. (Crested Wheatgrass) | | | | | | | | | | | | | | | |
| 1 | 2-day seedling | IEC | | + | ++ | | | | | | | | | + | 831 |
| *Agrostemma githago* L. (Cow Cockle) | | | | | | | | | | | | | | | |
| 1 | Embryo[g] | Lumin. | | | 0.7 | | | | | | | | | | 2453 |
| *Allium cepa* L. (Onion) | | | | | | | | | | | | | | | |
| 1 | Seed[g] | Lumin. | | | 0.30 | | | | | | | | | | 2454 |
| 1 | Leaf[d] | HPLC | 59.1 | 155.4 | 475.9 | | | | | | | | | | 2455 |
| 1 | –, minus parenchyma[d] | HPLC | 61.3 | 189.7 | 504.3 | | | | | | | | | | 2455 |
| 1 | –, minus vascular bundles[d] | HPLC | 45.0 | 145.9 | 575.0 | | | | | | | | | | 2455 |
| 1 | Bulb | IEC | 24 | | | | | | Trace | | | 15 | | | 2456 |
| 1 | Root[h] | Lumin. | 0.38 | 0.71 | 1.17 | | | | | | | | | | 2457 |
| *Allium fistulosum* L. (Welsh Onion) | | | | | | | | | | | | | | | |
| 1 | Bulb | IEC | 27 | | | | | | | | | 12 | | | 2456 |
| *Allium porrum* L. (Leek) | | | | | | | | | | | | | | | |
| 1 | Seed embryo[g] | HPLC | | | 0.250 | | | Trace | | | 0.030 | | | 0.100 | 2458 |
| *Alnus glutinosa* (L.) Gaertn. (Black Alder) | | | | | | | | | | | | | | | |
| 1 | Leaf bud[d] | Lumin. | 10 | 25 | 17 | | | | | | | | | | 2446 |
| *Alocasia odora* (Lodd.) Spach. (Asian Taro) | | | | | | | | | | | | | | | |
| 1 | Leaf (units unstated) | Lumin. | 0.15 | 0.35 | 0.96 | | | | | | | | | | 2459 |
| *Alyssum bertolonii* Desv. | | | | | | | | | | | | | | | |
| 1 | Seed[g] | Enzym. | 3.2 | 1.8 | 2.1 | | | | | | | | | | 2460 |
| *Amaryllis vittata* L'Her. (Amaryllis) | | | | | | | | | | | | | | | |
| 1 | Pollen | Enzym. | 4300 | 2030 | 330 | | | | | | | | | | 2461 |
| *Apium graveolens* (L.) ssp. *dulce* (Celery) | | | | | | | | | | | | | | | |
| 1 | Petiole, vascular bundle | PC/PC | | + | + | | | | | | | | | | 227 |
| *Arabidopsis thaliana* (L.) Heynh. (Mouse-Ear Cress) | | | | | | | | | | | | | | | |
| 1 | Leaf | | | 16.2 | 63.9 | | | | | | | | | 17.9 | 480 |
| *Arachis hypogaea* L. (Peanut) | | | | | | | | | | | | | | | |
| 1 | Seed[a] | Fluorometric | | | Low | | | | | | | | | | 2462 |
| 1 | –, embryonic axis[a] | Fluorometric | | | + | | | | | | | | | | 2463 |
| 1 | Leaf[i] | IEC | 27.5 | 11.5 | 45.0 | 4.0 | 27.0 | 16.0 | 25.0 | 17.0 | 55.0 | 2.0 | 18.0 | 10.5 | 2464 |

*nmol/g fwb unless stated otherwise. [a]Taken from the abstract. [b]μmol/L. [c]μg/plant part. [d]Dry weight basis. [e]nmol/$10^7$ cells. [f]ppm. [g]nmol/plant part. [h]nmol/mg insoluble polysaccharide. [i]μg/g. [j]μg/mL. [k]nmol/$10^6$ protoplasts. [l]μmol/$m^2$. [m]μmol/g. [n]μmol/$10^7$ cells. [o]nmol/mg protein. [p]nmol/mg chlorophyll. [q]Percentage of total free nucleotides. [r]m*M*. [s]mg/g. [t]Percentage P dwb. [u]Total extinction/callus (plant part). [v]counts per minute × $10^3$.

*Continued*

**Table 5-2** Ribonucleotides in Plants*—cont'd

| No. | Plant part | Method | AMP | ADP | ATP | GMP | GDP | GTP | CMP | CDP | CTP | UMP | UDP | UTP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Arachis hypogaea* L. ssp *fastigiata* (Spanish Peanut) | | | | | | | | | | | | | | | |
| 1 | Embryonic axis | Lumin. | 16.1 | 41.0 | 248.0 | | | | | | | | | | 2465 |
| *Arachis hypogaea* L. ssp *hypogaea* (Virginia Peanut) | | | | | | | | | | | | | | | |
| 1 | Embryonic axis | Lumin. | 16.8 | 41.0 | 138.3 | | | | | | | | | | 2465 |
| *Asparagus officinalis* L. (Asparagus) | | | | | | | | | | | | | | | |
| 1 | Green stem | IEC | 110 | | | Trace | | | 60 | | | 60 | | | 2456 |
| 1 | White stem | IEC | 70 | | | Trace | | | 40 | | | 80 | | | 2456 |
| 1 | Stem[d] | IEC | 780 | 690 | 940 | | | | | | | 2210 | | | 2466 |
| 1 | Stem (top, base) | Lumin. | | | + | | | | | | | | | | 2467 |
| 1 | Stem/shoot | HPLC | 48 | | | 6 | | | 3 | | | 84 | | | 2468 |
| *Avena fatua* L. (Wild Oat) | | | | | | | | | | | | | | | |
| 1 | Shoot[d,i] | Lumin. | | | 826.6 | | | | | | | | | | 2469 |
| 1 | 3-day seedling[j] | IEC | 93.5 | 12.5 | 24.0 | 32.5 | 49.0 | 10.0 | 46.5 | 7.5 | 29.0 | 19.0 | 23.0 | 7.5 | 2470 |
| *Avena sativa* L. (Oat) | | | | | | | | | | | | | | | |
| 1 | Seed[d] | Enzym. | | | 0 | | | | | | | | | | 232 |
| 1 | Seed | IEC | 35 | 47 | 76 | 0 | 7 | 8 | 0 | 4 | 8 | 38 | 30 | 26 | 2471 |
| 1 | Leaf, chloroplast[k] | Lumin. | 0.90 | 1.10 | 0.80 | | | | | | | | | | 2472 |
| 1 | –, mitochondria[k] | Lumin. | 0.22 | 0.56 | 0.85 | | | | | | | | | | 2472 |
| 1 | –, cytosol [k] | Lumin. | 0.02 | 0.90 | 1.85 | | | | | | | | | | 2472 |
| 1 | Seedling | IEC | 26.3 | 45.5 | 115.9 | 16.3 | 20.3 | 11.2 | 15.6* | 63.4 | 15.8 | 229.7 | 15.3 | 46.3 | 2473 |
| | *Incl. NAD | | | | | | | | | | | | | | |
| 1 | –, coleoptile | Lumin. | | | 121 | | | | | | | | | | 2474 |
| 1 | –, mesocotyl | Lumin. | | | 62 | | | | | | | | | | 2474 |
| 1 | –, root and stem | IEC | + | + | + | + | | | | | | + | | | 2475 |
| *Avicennia germinans* (L.) L. (Black Mangrove) | | | | | | | | | | | | | | | |
| 1 | Root[d] | Lumin. | 10 | 525 | 1115 | | | | | | | | | | 2476 |
| *Bambusa spinosa* Roxb. (Bamboo) | | | | | | | | | | | | | | | |
| 1 | Stalk | IEC | 33 | | | | | | 15 | | | 40 | | | 2456 |
| *Beta vulgaris* L. (Sugar Beet) | | | | | | | | | | | | | | | |
| 1 | Seed[g] | Lumin. | | | 0.04 | | | | | | | | | | 2477 |
| 2 | Seed embryo | TLC | + | + | + | | | | | | | + | + | + | 2478 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2 | Seed embryo[g] | Enzym. | | | | | | | | | | 0.179-0.202 | 2478 |
| 2 | Axis | Lumin. | | | 0.35-0.50 | | | Other NTP 0.40-0.50 | | | | | 481 |
| 1 | Leaf | PC/PC | 8.8 | 15.3 | 26.5 | | | | 18.6 | 14.1 | 8.2 | | 2479 |
| 1 | –, vascular bundle | PC/PC | 17.0 | 7.2 | 9.7 | | | | 19.3 | 30.0 | 7.2 | | 2479 |
| 1 | –, petiole parenchyma | PC/PC | 2.8 | 0 | 2.1 | | | | 8.0 | 6.3 | 2.4 | | 2479 |
| 1 | Leaf[d] | HPLC | 259 | 419 | 802 | | | | | | | | 2480 |
| 1 | –, chloroplast[d] | Enzym. | 1010 | 1230 | 790 | | | | | | | | 2481 |
| 1 | Leaf | Lumin. | 238 | 542 | 583 | | | | | | | | 2482 |
| 3 | Leaf[l] | Lumin. | | | 1420-2600 | | and variation among upper, middle, and lower leaves | | | | | | 2483 |
| 1 | Root | Lumin. | | | 11.8 | | | | | | | | 2484 |
| 1 | Root[i] | IEC | 1570.6 | + | 2584.7 | 23.5 | + | + | 1403.5 | | | | 2485 |
| 1 | Taproot [d] | HPLC | | <100 | | | | | | 7200 | | | 2486 |
| 1 | Fibrous root[d] | HPLC | | 400 | | | 165 | | | 1030 | | | 2486 |
| *Betula costata* Trautv. | | | | | | | | | | | | | |
| 1 | Sap[a] | | + | | | + | | + | + | | | | 2451 |
| *Betula davurica* Pall. | | | | | | | | | | | | | |
| 1 | Sap[a] | | + | | | + | | + | + | | | | 2451 |
| *Betula ermanii* Cham. | | | | | | | | | | | | | |
| 1 | Bark[d] | Lumin. | | | 152 | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 56 | | | | | | | | 2487 |
| *Betula nigra* L. (River Birch) | | | | | | | | | | | | | |
| 1 | Root[d] | Lumin. | 0.1 | 0.4 | 1.8 | | | | | | | | 2488 |
| *Betula pendula* Roth (European White Birch) | | | | | | | | | | | | | |
| 1 | Root[d] | Lumin. | 0.1 | 0.3 | 1.2 | | | | | | | | 2488 |

*nmol/g fwb unless stated otherwise. [a]Taken from the abstract. [b]µmol/L. [c]µg/plant part. [d]Dry weight basis. [e]nmol/$10^7$ cells. [f]ppm. [g]nmol/plant part. [h]nmol/mg insoluble polysaccharide. [i]µg/g. [j]µg/mL. [k]nmol/$10^6$ protoplasts. [l]µmol/$m^2$. [m]µmol/g. [n]µmol/$10^7$ cells. [o]nmol/mg protein. [p]nmol/mg chlorophyll. [q]Percentage of total free nucleotides. [r]m*M*. [s]mg/g. [t]Percentage P dwb. [u]Total extinction/callus (plant part). [v]counts per minute × $10^3$.

*Continued*

**Table 5-2** Ribonucleotides in Plants*—cont'd

| No. | Plant part | Method | AMP | ADP | ATP | GMP | GDP | GTP | CMP | CDP | CTP | UMP | UDP | UTP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Betula platyphylla* Suk. (Asian White Birch) | | | | | | | | | | | | | | | |
| 1 | Sap[a] | | + | | | + | | | + | | | + | | | 2451 |
| *Bidens pilosa* L. (Bur Marigold) | | | | | | | | | | | | | | | |
| 1 | Cotyledon[g] | Lumin. | | | 0.722 | | | | | | | | | | 2489 |
| *Brassica campestris* L. (Turnip Rape) | | | | | | | | | | | | | | | |
| 1 | Leaf[a] | | | | + | | | | | | | | | | 2490 |
| *Brassica chinensis* L. (Pak-Choi) | | | | | | | | | | | | | | | |
| 1 | Seed[a] | Fluorometric | | | + | | | | | | | | | | 2491 |
| *Brassica napus* L. ssp. *oleifera* (Winter Rape) | | | | | | | | | | | | | | | |
| 1 | Seed[g] | Lumin. | 1.47 | 0.33 | 0.18 | | | | | | | | | | 2477 |
| 1 | Leaf[d] | Lumin. | 220 | 640 | 660 | | | | | | | | | | 2492 |
| 1 | Leaf[i] | Lumin. | | | 107 | | | | | | | | | | 2493 |
| 1 | Shoot apex[i] | Lumin. | | | 166 | | | | | | | | | | 2493 |
| 1 | Root[d,i] | Lumin. | | | 157.2 | | | | | | | | | | 2494 |
| *Brassica nigra* (L.) Koch (Black Mustard) | | | | | | | | | | | | | | | |
| 1 | Leaf petiole cell suspension | Enzym. | | 4.7 | 36 | | | | | | | | | | 485 |
| *Brassica oleracea* L. ssp. *botrytis* L. (Cauliflower) | | | | | | | | | | | | | | | |
| 1 | Seed[g] | Lumin. | | | 0.02 | | | | | | | | | | 2477 |
| 1 | Flowerhead | HPLC | 8 | | | 99 | | | n.d. | | | 37 | | | 2468 |
| *Brassica oleracea* L. ssp. *capitata* L. (Cabbage) | | | | | | | | | | | | | | | |
| 1 | Seed[d] | Lumin. | 513.5 (incl. ADP and ATP) | | | | | | | | | | | | 2495 |
| 1 | Leaf[i] | IEC | 6 | – | – | – | | | 5 | | | 6 | | | 2496 |
| 1 | Leaf | HPLC | 3 | | | n.d. | | | n.d. | | | 36 | | | 2468 |
| *Brassica oleracea* L. ssp. *caulorapa* (Kohlrabi) | | | | | | | | | | | | | | | |
| 1 | Seed[g] | Lumin. | | | 0.53 | | | | | | | | | | 2454 |
| *Brassica oleracea* L. ssp. *italica* Plenck. (Broccoli) | | | | | | | | | | | | | | | |
| 1 | Stems and florets | HPLC | n.d. | 131 | 149 | 21 | 29 | 51 | 147 | 152 | 196 | 92 | 71 | 183 | 2441 |
| 1 | Flowerhead | HPLC | 9 | | | n.d. | | | n.d. | | | 32 | | | 2468 |
| *Brassica pekinensis* (Lour.) Rupr. (Chinese Cabbage, Pe-Tsai) | | | | | | | | | | | | | | | |
| 1 | Seed[g] | Lumin. | 14400 | 2500 | 1000 | | | | | | | | | | 2497 |
| 1 | Seed | Fluorometric | | | + | | | | | | | | | | 2491 |
| 1 | Leaf[i] | IEC | 6 | 2 | 5 | 7 | | | 4 | | | 11 | | | 2496 |
| 1 | Stem | PC/PC | 2.3 | 1.6 | 0.04 | | 0.2 | | | 0.2 | | 0.5 | | | 2498 |
| 1 | –, vascular bundle | PC/PC | | + | + | | + | + | | | | + | + | + | 36 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, vascular bundle | TLC/TLC | | + | + | | + | + | | | | + | + | + | 36 |
| 1 | –, vascular bundle | TLC/TLE | | + | + | | | + | | | | + | + | | 36 |
| *Brassica rapa* L. (Turnip Rape) | | | | | | | | | | | | | | | |
| 1 | Seed[d] | Lumin. | 312.5 (incl. ADP and ATP) | | | | | | | | | | | | 2495 |
| 1 | Leaf vascular bundle | TLC/TLC | | + | + | | | | | | | | | + | 240 |
| *Camellia sinensis* L. (Tea) | | | | | | | | | | | | | | | |
| 3 | Green leaf[i] | IEC | 83-104 | + | | + | | | | | | 151-216 | | | 2499 |
| *Camellia sinensis* L. ssp. *assamica* (Mast.) Kitam. (Assam Tea) | | | | | | | | | | | | | | | |
| 1 | Shoot | IEC | | 41 | 100 | | | | | | 9 | 11 | 15 | 32 | 2500 |
| 1 | Shoot | Enzym. | 2 | 51 | 80 | | | | | | | | | | 2500 |
| *Cannabis sativa* L. (Hemp) | | | | | | | | | | | | | | | |
| 1 | Leaf[d,i] | IEC | 11.3 | 15.4 | 15.5 | | | | | | | | | | 2501 |
| *Capsicum annuum* L. (Bell Pepper) | | | | | | | | | | | | | | | |
| 1 | Seed[g] | Lumin. | | | 0.44 | | | | | | | | | | 2454 |
| 1 | Leaf[d] | Lumin. | | | 730 | | | | | | | | | | 2502 |
| 1 | Leaf, mature | HPLC | 11 | 34 | 30 | | | | | | | 13 | 7 | 8 | 2503 |
| 1 | –, young | HPLC | 19 | 74 | 160 | | | | | | | 62 | 34 | 82 | 2503 |
| 1 | –, petiole | HPLC | 5 | 17 | 26 | | | | | | | 31 | 5 | 13 | 2503 |
| 1 | Fruit | HPLC | | ++ | ++ | + | + | | | + | | ++ | + | + | 2441 |
| 1 | Fruit | HPLC | 2 | | | n.d. | | | n.d. | | | 19 | | | 2468 |
| *Carpinus betulus* L. (European Hornbeam) | | | | | | | | | | | | | | | |
| 1 | Phloem exudate[b] | Enzym. | | | 94 | | | | | | | | | | 2444 |
| *Carthamus tinctorius* L. (Safflower) | | | | | | | | | | | | | | | |
| 1 | Seed | Fluorometric | | | + | | | | | | | | | | 2491 |
| 1 | Leaf | HPLC | 3 | 16 | 11 | | | | | | | 17 | 5 | 10 | 2503 |
| 1 | Flower bud | HPLC | 4 | 29 | 43 | | | | | | | 28 | 13 | 30 | 2503 |
| *Catharanthus roseus* (L.) G. Don (Madagascar Periwinkle) | | | | | | | | | | | | | | | |
| 1 | Cell suspension culture[d,e] | Enzym. | 49 | 87 | 21 | | | | | | | | | | 2504 |
| 1 | Cell suspension culture | HPLC | 15.9 | 17.5 | 100.7 | 2.7 | 2.6 | 26.1 | 5.6 | 4.1 | 7.3 | 32.7 | 29.3 | 55.0 | 2505 |

*nmol/g fwb unless stated otherwise. [a]Taken from the abstract. [b]µmol/L. [c]µg/plant part. [d]Dry weight basis. [e]nmol/$10^7$ cells. [f]ppm. [g]nmol/plant part. [h]nmol/mg insoluble polysaccharide. [i]µg/g. [j]µg/mL. [k]nmol/$10^6$ protoplasts. [l]µmol/$m^2$. [m]µmol/g. [n]µmol/$10^7$ cells. [o]nmol/mg protein. [p]nmol/mg chlorophyll. [q]Percentage of total free nucleotides. [r]m*M*. [s]mg/g. [t]Percentage P dwb. [u]Total extinction/callus (plant part). [v]counts per minute × $10^3$.

*Continued*

**Table 5-2** Ribonucleotides in Plants*—cont'd

| No. | Plant part | Method | AMP | ADP | ATP | GMP | GDP | GTP | CMP | CDP | CTP | UMP | UDP | UTP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Cell suspension culture[e] | Lumin. | | | 2.1 | | | | | | | | | | 2506 |
| 1 | Cell suspension culture (*in vivo*) | $^{31}$P NMR | | + | + | | | | | | | | | | 2507 |
| *Chenopodium rubrum* L. (Red Goosefoot) | | | | | | | | | | | | | | | |
| 1 | Seedling | Lumin. | | | + | | | | | | | | | | 2508 |
| 1 | Cell suspension culture | Enzym. | 4 | 15 | 42 | | | | | | | <1 | 1 | 5 | 2509 |
| *Chrysanthemum* spp. (Chrysanthemum) | | | | | | | | | | | | | | | |
| 1 | Leaf[i] | IEC | | 286 | 217 | 201 | 88 | 105 | 176 | 52 | 258 | 211 | 250 | 188 | 2510 |
| *Cicer arietinum* L. (Chickpea) | | | | | | | | | | | | | | | |
| 1 | Seedling, cotyledon[g] | Enzym. | 105 | 10 | 575 | | | | | | | | | | 247 |
| 1 | –, embryonic axis[g] | Enzym. | 1.5 | 3.5 | 11.5 | | | | | | | | | | 247 |
| *Cichorium intybus* L. (Chicory) | | | | | | | | | | | | | | | |
| 1 | Explant leaf[d,g] | IEC | 32 | | | 50 | | | 32 | | | 45 | | | 2511 |
| *Citrullus vulgaris* Schrad. (Watermelon) | | | | | | | | | | | | | | | |
| 1 | Seed[a] | PC/PE | | | | | | | | | | + | | | 2512 |
| *Citrus aurantium* L. (Sour Orange) | | | | | | | | | | | | | | | |
| 1 | Fruit juice[b] | Lumin. | | | 7.67 | | | | | | | | | | 2513 |
| –, var. "Bittersweet" (Bittersweet Orange) | | | | | | | | | | | | | | | |
| 1 | Fruit juice[b] | Lumin. | | | 87.91 | | | | | | | | | | 2513 |
| *Citrus grandis* (L.) Osbeck (Pummelo) | | | | | | | | | | | | | | | |
| 2 | Fruit juice[b] | Lumin. | | | 22.67-135.20 | | | | | | | | | | 2513 |
| *Citrus limettioides* Tanaka (Sweet Lemon) | | | | | | | | | | | | | | | |
| 1 | Fruit pulp | IEC | 7.0 | 27.0 | 18.5 | | | | | | | | | | 2514 |
| *Citrus limon* L. (Lemon) | | | | | | | | | | | | | | | |
| 1 | Leaf[d] | PC/PE | 8600 | 4200 | 1800 | | | | | | | | | | 2515 |
| 1 | Fruit pulp | IEC | 5.5 | 21.3 | 15.8 | | | | | | | | | | 2514 |
| *Citrus limonia* Osbeck (Lime) | | | | | | | | | | | | | | | |
| 2 | Fruit juice[b] | Lumin. | | | 3.27-4.89 | | | | | | | | | | 2513 |
| *Citrus natsudaidai* Hayata (Sour Orange) | | | | | | | | | | | | | | | |
| 1 | Leaf | Lumin. | | | 200 | | | | | | | | | | 2516 |
| 1 | Juice vesicle | Lumin. | | | 1910 | | | | | | | | | | 2516 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Citrus paradisi* Macf. (Grapefruit) | | | | | | | | | | | | | | | |
| 2 | Fruit juice[b] | Lumin. | | | 9.79-40.20 | | | | | | | | | | 2513 |
| *Citrus paradisi* Macf. × *Citrus reticulata* Blanco (Tangelo) | | | | | | | | | | | | | | | |
| 1 | Peeled pulp vesicles[i] | IEC | 0.6-7.7 | 0-3.3 | | 0-0.3 | | | | n.d. | | 0-1.0 | | | 2517 |
| 1 | Peeled pulp vesicles[i] | Lumin. | | | 20.6-25.8 | | | | | | | | | | 2517 |
| *Citrus reticulata* × *Fortunella* spp. (Calamondin) | | | | | | | | | | | | | | | |
| 1 | Fruit juice[b] | Lumin. | | | 3.34 | | | | | | | | | | 2513 |
| *Citrus reticulata* × *Citrus sinensis* (Murcott) | | | | | | | | | | | | | | | |
| 1 | Fruit juice[b] | Lumin. | | | 91.50 | | | | | | | | | | 2513 |
| *Citrus sinensis* (L.) Osbeck (Orange) | | | | | | | | | | | | | | | |
| 1 | Juice | IEC | + | + | + | | + | + | + | + | + | + | + | + | 248 |
| 4 | Juice[j] | HPLC | 0.5-1.8 | 6.0-26.0 | 1.6-5.4 | 0.2-1.4 | 0.8-4.3 | 0.2-0.9 | 0.8-2.8 | 2.8-19.0 | 0.4-0.9 | 0.3-1.8 | 2.3-7.6 | 0.3-2.3 | 2518 |
| 1 | Juice[b] | Lumin. | | | 64.90 | | | | | | | | | | 2513 |
| 1 | Juice vesicles[i] *Incl. GTP | IEC | 1.8 | 0.2 | 2.0 | 2.2 | | | 4.6 (incl. NAD) | | | 1.9 | 0.7 | 21.9* | 2519 |
| 2 | Peeled pulp vesicles[i] | IEC | 0.3-5.0 | | | 0.9 | | | 0.3-5.6 | | | 0.8-1.2 | | | 2517 |
| 2 | Peeled pulp vesicles[i] | Lumin. | | | 5.2-19.9 | | | | | | | | | | 2517 |
| 1 | Juice vesicles, mature[b] | Enzym. | | + | 66 | | | | | | | | | | 2520 |
| 1 | –, immature[b] | Enzym. | | + | 151 | | | | | | | | | | 2520 |
| *Citrus sinensis* × *Citrus reticulata* (Orangeuma) | | | | | | | | | | | | | | | |
| 1 | Fruit juice[b] | Lumin. | | | 127.60 | | | | | | | | | | 2513 |
| *Cladrastis lutea* (Michx.f.) Koch (Yellowwood) | | | | | | | | | | | | | | | |
| 1 | Phloem exudate[b] | Enzym. | | | 310 | | | | | | | | | | 2444 |
| *Coleus shirensis* Gürke | | | | | | | | | | | | | | | |
| 1 | Leaf chloroplast[d] | Enzym. | 840 | 440 | 480 | | | | | | | | | | 2481 |

*nmol/g fwb unless stated otherwise. [a]Taken from the abstract. [b]μmol/L. [c]μg/plant part. [d]Dry weight basis. [e]nmol/$10^7$ cells. [f]ppm. [g]nmol/plant part. [h]nmol/mg insoluble polysaccharide. [i]μg/g. [j]μg/mL. [k]nmol/$10^6$ protoplasts. [l]μmol/$m^2$. [m]μmol/g. [n]μmol/$10^7$ cells. [o]nmol/mg protein. [p]nmol/mg chlorophyll. [q]Percentage of total free nucleotides. [r]m*M*. [s]mg/g. [t]Percentage P dwb. [u]Total extinction/callus (plant part). [v]counts per minute × $10^3$.

*Continued*

**Table 5-2** Ribonucleotides in Plants*—cont'd

| No. | Plant part | Method | AMP | ADP | ATP | GMP | GDP | GTP | CMP | CDP | CTP | UMP | UDP | UTP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Corchorus capsularis* L. (Jute) | | | | | | | | | | | | | | | |
| 1 | Seed | Enzym. | 46.5 | 77.4 | 30.7 | | | | | | | | | | 2521 |
| *Corylus avellana* L. (European Hazel) | | | | | | | | | | | | | | | |
| 1 | Seed[d] | IEC | 215 | 12 | 3 | | | | | | | 155 | | | 2522 |
| *Costus speciosus* (J. Kõnig) Sm. (Crepe Ginger) | | | | | | | | | | | | | | | |
| 1 | Cell suspension culture | HPLC | 26 | 48 | 158 | | | + | + | | + | | | | 2523 |
| *Cucumis melo* L. (Melon) | | | | | | | | | | | | | | | |
| 1 | Seed[a] | PC/PE | | | | | | | | | | + | | | 2512 |
| *Cucumis sativus* L. (Cucumber) | | | | | | | | | | | | | | | |
| 1 | Seed[g] | Lumin. | | | 3.16 | | | | | | | | | | 2454 |
| 1 | Cotyledon[d] | Lumin. | 65 | 60 | 0 | | | | | | | | | | 2524 |
| 1 | Leaf | IEC | | | 29.1 | | | | | | | | | | 250 |
| 1 | Leaf | Enzym. | | | 530 | | | | | | | | | | 2525 |
| 1 | Leaf | Lumin. | 108 | 101 | 39 | | | | | | | | | | 2526 |
| 1 | Fruit | IEC | 130 | | | | | | Trace | | | 20 | | | 2456 |
| 1 | Seedling | IEC | | + | + | | | | | | | | | | 2527 |
| 1 | Root | Enzym. | | | 440 | | | | | | | | | | 2525 |
| 1 | Root | Lumin. | 86 | 35 | 10 | | | | | | | | | | 2526 |
| *Cucurbita maxima* Duch. (Squash) | | | | | | | | | | | | | | | |
| 1 | Seed, cotyledon | Enzym. | 19 | 74 | 290 | | | | | | | | | | 2528 |
| 1 | Leaf, sieve-tube exudate | TLC/TLC | | + | + | | | | | | | | | + | 240 |
| *Cucurbita pepo* L. (Pumpkin) | | | | | | | | | | | | | | | |
| 1 | Young leaf | Lumin. | | | 11800 | | | | | | | | | | 2529 |
| 1 | Leaf[d,m] | IEC | 2.0 | 1.5 | 2.4 | 1.4 | 1.8 | 1.1 | 3.8 | | | 2.4 | 1.9 | 0.7 | 2530 |
| 1 | –, chloroplast[d,m] | IEC | 0.3 | 0.6 | 0.6 | | | | | | | | | | 2530 |
| 1 | Leaf mitochondria[d] | IEC | 406 | 2779 | 302 | | | | | | | | | | 1633 |
| 1 | Stem exudate[b] | IEC | 129 | 8 | 549 | 5 | 27 | 207 | | | | 7 | 115 | 101 | 251 |
| 1 | Unripe fruit exudate[b] | IEC | 34 | 28 | 147 | 3 | 3 | 12 | | | | 4 | 84 | 33 | 251 |
| 1 | Ripe fruit exudate [b] | IEC | 74 | 8 | 333 | 28 | 51 | 127 | | | | 43 | 293 | 549 | 251 |
| 1 | Sieve tube exudate[b] | Lumin. | | | 17.6-32.9 | | | | | | | | | | 2531 |
| 1 | Root | IEC | 16.6 | 20.7 | 1.4 | 9.9 | 7.6 | | 2.7 | | | 14.3 | 0.7 | | 2532 |
| 1 | Root, meristem[n] | IEC | 1.2 | 4.8 | 0.5 | 1.2 | 3 | | 2.1 | | | 2.2 | 4.4 | | 2533 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, growth zone[n] | IEC | 1.2 | 22.6 | 1.6 | 2.8 | 6.2 | | 6.2 | | | 12.2 | 3.1 | | 2533 |
| 1 | –, hair zone[n] | IEC | 2.5 | 28.3 | 1.5 | 4.4 | 25.2 | | 15 | | | 7.6 | 22 | | 2533 |
| *Cyclobalanopsis globosa* Lin and Liu | | | | | | | | | | | | | | | |
| 1 | Seed[a,d] | – | + | | >20 | | | | | | | | | | 2534 |
| *Datura inoxia* Mill. (Downy Thorn Apple) | | | | | | | | | | | | | | | |
| 1 | Tissue culture | HPLC[3465] | 22.2 | 16.2 | 37.4 | 31.9 | 10.8 | 18.5 | n.d. | 5.4 | 7.4 | 5.9 | 11.5 | 25.4 | 2535 |
| 1 | Cell suspension culture | HPLC | 2.2 | 7.1 | 46 | 0.4 | 1.8 | 11.0 | | | 2.2 | 12.7 | 2.4 | 13.1 | 2440 |
| *Daucus carota* L. (Carrot) | | | | | | | | | | | | | | | |
| 1 | Root | IEC | + | | | 0 | | | | | | + | + | | 2536 |
| 1 | Cell suspension culture | TLC/TLC | | | 65 | | | 18 | | | | | | | 2537 |
| 1 | Cell suspension culture | HPLC | | 70 | 300 | | 25 | 95 | | n.d. | n.d. | | 35 | 95 | 2538 |
| 1 | Cell suspension culture (*in vivo*) | $^{31}$P NMR | | + | + | | | | | | | | | | 2507 |
| 1 | Callus suspension culture[l] | Lumin. | 0.065 | 0.10 | 0.21 | | | | | | | | | | 2539 |
| *Digitalis lanata* Ehrh. (Grecian Foxglove) | | | | | | | | | | | | | | | |
| 1 | Leaf[l] | Lumin. | 8.0 | 12.5 | 33.5 | | | | | | | | | | 2540 |
| *Diospyros kaki* Thunb. (Persimmon) | | | | | | | | | | | | | | | |
| 1 | Leaf tea[a] | – | + | | | + | | | ++ | | | + | | | 2541 |
| *Distichlis spicata* (L.) Greene (Coastal Saltgrass) | | | | | | | | | | | | | | | |
| 1 | Leaf[d] | Lumin. | 27 | 74 | 160 | | | | | | | | | | 2542 |
| *Drimys lanceolata* (Poir.) Baill. (Pepper Tree) | | | | | | | | | | | | | | | |
| 1 | Leaf | IEC | 11.3 | 12.1 | | 9.4 | 20.2 | 1.6 | 5.2 | | | | Trace | | 2543 |
| *Echinochloa cruz-galli* Beauv. ssp. *praticola* (Barnyard Grass) | | | | | | | | | | | | | | | |
| 1 | Seed[a] | – | | | + | | | | | | | | | | 2544 |
| *Egeria densa* Planch. (Brazilian Waterweed) | | | | | | | | | | | | | | | |
| 1 | Leaf | PC/PC | | | + | | | | | | | | | | 2545 |
| 1 | Leaf | Enzym. | | 20 | 73 | | | | | | | | | | 495 |
| 1 | Shoot[d] | Enzym. | | | 700 | | | | | | | | | | 2481 |
| 1 | –, cytoplasm[d] | Enzym. | | | 3200 | | | | | | | | | | 2481 |

*nmol/g fwb unless stated otherwise. [a]Taken from the abstract. [b]μmol/L. [c]μg/plant part. [d]Dry weight basis. [e]nmol/$10^7$ cells. [f]ppm. [g]nmol/plant part. [h]nmol/mg insoluble polysaccharide. [i]μg/g. [j]μg/mL. [k]nmol/$10^6$ protoplasts. [l]μmol/$m^2$. [m]μmol/g. [n]μmol/$10^7$ cells. [o]nmol/mg protein. [p]nmol/mg chlorophyll. [q]Percentage of total free nucleotides. [r]m*M*. [s]mg/g. [t]Percentage P dwb. [u]Total extinction/callus (plant part). [v]counts per minute × $10^3$.

*Continued*

**Table 5-2** Ribonucleotides in Plants*—cont'd

| No. | Plant part | Method | AMP | ADP | ATP | GMP | GDP | GTP | CMP | CDP | CTP | UMP | UDP | UTP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Episcia reptans* Mart. (Flame Violet) | | | | | | | | | | | | | | | |
| 1 | Leaf[d] | Lumin. | 560 | 410 | 200 | | | | | | | | | | 2546 |
| *Evodia rutaecarpa* Hook.f. and Thomps. (Evodia) | | | | | | | | | | | | | | | |
| 1 | Phloem exudate[b] | Enzym. | | | 350 | | | | | | | | | | 2444 |
| *Fagopyrum esculentum* Moench (Buckwheat) | | | | | | | | | | | | | | | |
| 1 | Seed[i] | Lumin. | | | 12.6 | | | | | | | | | | 2547 |
| 1 | Seedling[a] | | | + | + | | | | | | | | | | 2548 |
| *Fagus sylvatica* L. (European Beech) | | | | | | | | | | | | | | | |
| 1 | Leaf bud[d] | Lumin. | 10 | 8 | 4 | | | | | | | | | | 2446 |
| 1 | Phloem exudate[b] | Enzym. | | | 260 | | | | | | | | | | 2444 |
| *Festuca arundinacea* Schreb. (Reed Fescue) | | | | | | | | | | | | | | | |
| 1 | Leaf | Lumin. | | | 0.033 | | | | | | | | | | 2549 |
| *Festuca pratensis* L. (Meadow Fescue) | | | | | | | | | | | | | | | |
| 1 | Leaf | Lumin. | | | 0.125 | | | | | | | | | | 2549 |
| *Ficaria verna* Huds. (Lesser Celandene) | | | | | | | | | | | | | | | |
| 1 | Tuber[i] | TLC/TLC | 16 | 50 | 155 | | | | | | | | | | 2550 |
| *Fragaria* spp. (Strawberry) | | | | | | | | | | | | | | | |
| 1 | Leaf | IEC | | 59 | 98 | | 11 | 14.4 | 3 | 6 | 18 | 8.4 | 28 | 40 | 259 |
| 1 | Leaf | Enzym. | | 65 | 92 | | | | | | | | | | 259 |
| *Fraxinus americana* L. (White Ash) | | | | | | | | | | | | | | | |
| 1 | Phloem exudate[b] | Enzym. | | | 590 | | | | | | | | | | 2444 |
| 1 | Phloem exudate[b] | TLC/TLC | | | + | | | 0 | | | | | | 0 | 2444 |
| *Fraxinus excelsior* L. (European Ash) | | | | | | | | | | | | | | | |
| 1 | Leaf bud[d] | Lumin. | 0 | 15 | 17 | | | | | | | | | | 2446 |
| 1 | Apical bud[o] | Lumin. | | | 2.0 | | | (Other NTP 3.3) | | | | | | | 2551 |
| 1 | Phloem exudate[b] | Enzym. | | | 270 | | | | | | | | | | 2444 |
| *Fraxinus mandshurica* Rupr. ssp. *japonica* Maxim. (Japanese Ash) | | | | | | | | | | | | | | | |
| 1 | Bark[d] | Lumin. | | | 150 | | | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 43 | | | | | | | | | | 2487 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ginkgo biloba* L. (Ginkgo) | | | | | | | | | | | | | | | |
| 1 | Bark[d] | Lumin. | | | 83 | | | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 7 | | | | | | | | | | 2487 |
| *Glycine max* (L.) Merr. (Soybean) | | | | | | | | | | | | | | | |
| 1 | Seed[d] *Incl. UTP | IEC | 290 | 40 | 110 | 40 | 0 | 80* | 0 | | 180 | 90 | 70 | | 2552 |
| 1 | Seed | IEC | 26.0 | 28.0 | 34.7 | 0.3 | | Trace | | | | + | 2.6 | | 2553 |
| 1 | Seed[c,d] | Lumin. | 22 | 2 | 1 | | | | | | | | | | 2554 |
| 1 | Seed[d] | Lumin. | 584.0 (incl. ADP and ATP) | | | | | | | | | | | | 2495 |
| 1 | Seed[i] | Lumin. | | | 11.4 | | | | | | | | | | 2555 |
| 2 | –, axis[d,i] | Lumin. | | | 0.65-2.57 | | | | | | | | | | 2556 |
| 2 | –, cotyledon[d,i] | Lumin. | | | 0.20-1.04 | | | | | | | | | | 2556 |
| 7 | Embryonic axis[g] | Lumin. | | | 2.98-4.28 | | | | | | | | | | 2557 |
| 1 | Leaf[p] | HPLC | 8 | 96 | 124 | | | | | | | | 8 | 40 | 26 |
| 1 | Leaf[d] | IEC | 150 | 1000 | 1280 | | | | | | | | | | 2558 |
| 1 | Leaf | Lumin. | 89 | 357 | 464 | | | | | | | | | | 2482 |
| 7 | Leaf[o] | Lumin. | | | 16.6-30.9 | | | | | | | | | | 2559 |
| 1 | Sprout | IEC | 66 | | | | | | | | | 21 | | | 2456 |
| 1 | 3-day seedling, hypocotyl | IEC | + | + | + | + | | + | | | + | + | + | + | 2560 |
| 1 | Fruit, cotyledon[d] | Lumin. | 750 (incl. ADP and ATP) | | | | | | | | | | | | 2561 |
| 1 | –, seed coat[d] | Lumin. | 1300 (incl. ADP and ATP) | | | | | | | | | | | | 2561 |
| 1 | –, pod wall[d] | Lumin. | 300 (incl. ADP and ATP) | | | | | | | | | | | | 2561 |
| 1 | Root[j] | IEC | 60 | 1130 | 3600 | | | | | | | | | | 2558 |
| 1 | Root | HPLC (lumin.) | 7 (18) | 2 (3) | 45 (67) | | | + | | + | | | | | 2562 |
| 1 | Nodule | HPLC | 259 | 140 | 134 | | | + | | + | + | + | | | 2562 |
| 1 | Nodule (*in vivo*) | $^{31}$P NMR | | | ~350 | | | | | | | | | | 2563 |
| 1 | Nodule | Lumin. | 14.4 | 102.0 | 148.1 | | | | | | | | | | 2564 |
| 1 | –, host cell fraction | Lumin. | 8.1 | 86.7 | 103.5 | | | | | | | | | | 2564 |
| 1 | –, bacteroid fraction | Lumin. | 6.3 | 15.3 | 44.6 | | | | | | | | | | 2564 |
| 1 | Root | Enzym. | 4.4 | 14.1 | 37.7 | | | | | | | | | | 2565 |
| 1 | –, nodule | Enzym. | 61.4 | 121 | 186 | and distribution within the nodule | | | | | | | | | 2565 |

*nmol/g fwb unless stated otherwise. [a]Taken from the abstract. [b]µmol/L. [c]µg/plant part. [d]Dry weight basis. [e]nmol/$10^7$ cells. [f]ppm. [g]nmol/plant part. [h]nmol/mg insoluble polysaccharide. [i]µg/g. [j]µg/mL. [k]nmol/$10^6$ protoplasts. [l]µmol/$m^2$. [m]µmol/g. [n]µmol/$10^7$ cells. [o]nmol/mg protein. [p]nmol/mg chlorophyll. [q]Percentage of total free nucleotides. [r]m*M*. [s]mg/g. [t]Percentage P dwb. [u]Total extinction/callus (plant part). [v]counts per minute × $10^3$.

*Continued*

**Table 5-2** Ribonucleotides in Plants*—cont'd

| No. | Plant part | Method | AMP | ADP | ATP | GMP | GDP | GTP | CMP | CDP | CTP | UMP | UDP | UTP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Gossypium arboreum* L. (Tree Cotton) | | | | | | | | | | | | | | | |
| 1 | Immature boll, seed, hair[g] | CC (cellulose) | 40 | 78 | 20 | | | | | | | 88 | 57 | 47 | 2566 |
| 1 | Ovule[d] | Enzym. | 128 | 50 | 353 | | | | | | | | | | 2567 |
| 1 | Seed hair (lint)[d] | Enzym. | 127 | 137 | 413 | | | | | | | | | | 2567 |
| *Gossypium hirsutum* L. (Upland Cotton) | | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | + | + | + | | | | | | | | | | 2568 |
| 1 | Seed[a] | Fluorometric | | | + | | | | | | | | | | 2491 |
| 1 | Leaf[d] | IEC | 331 | 439 | 444 | | | | | | | 137 | 972 | 166 | 2569 |
| 1 | Leaf chloroplast[a] | | + | + | 0 | + | | + | | | | + | | + | 2570 |
| 1 | Raw fiber | IEC | + | + | + | + | + | + | | | | | + | + | 2571 |
| 1 | Raw fiber | HPLC | + | + | + | + | + | + | | | | + | + | + | 2571 |
| 1 | Ovule[d] | Enzym. | 136 | 60 | 362 | | | | | | | | | | 2567 |
| 1 | Seed hair (lint)[d] | Enzym. | 217 | 103 | 401 | | | | | | | | | | 2567 |
| 1 | Root[d] | IEC | 162 | 478 | 849 | | | | | | | 80 | 1387 | 676 | 2569 |
| 1 | Seedling, leaf *Incl. UDPG | IEC | 114 | 139 | 169 | 42.4 | 30.6 | 84.2 | 8.4 | Trace | 53.8 | 40.5 | 246* | 37.3 | 2572 |
| 1 | –, root *Incl. UDPG | IEC | 82 | 53.2 | 166.5 | 12.8 | 15.5 | 70.5 | 3.8 | Trace | 53.2 | 30.3 | 438* | 17 | 2572 |
| 2 | Seedling, root[d] | Lumin. | 0.08 | 0.38-0.63 | 0.72-0.97 | | | | | | | | | | 3104 |
| *Hedera helix* L. (English Ivy) | | | | | | | | | | | | | | | |
| 1 | Leaf | HPLC | 29.2 | 30.1 | 42.7 | 15.3 | 7.8 | 7.2 | 6.3 | 5.0 | 19.8 | 25.4 | 21.5 | 18.7 | 2573 |
| *Helianthus annuus* L. (Sunflower) | | | | | | | | | | | | | | | |
| 1 | Seed[d] | Lumin. | 177.1 (incl. ADP and ATP) | | | | | | | | | | | | 2495 |
| 1 | Leaf[l] | Lumin. | 7.4 | 13.5 | 19.8 | | | | | | | | | | 2574 |
| 1 | Leaf[d] | IEC | 10 | 680 | 800 | | | | | | | | | | 2558 |
| 1 | Stem | $^{31}$P NMR | | | + | | | | | | | | | | 2563 |
| 1 | Root[d] | $^{31}$P NMR | 40 | 220 | 730 | | | | | | | | | | 2558 |
| *Helianthus tuberosus* L. (Jerusalem Artichoke) | | | | | | | | | | | | | | | |
| 1 | Shoot | Lumin. | 9.0 | 4.2 | 63.0 | | | | | | | | | | 2575 |
| 1 | Young stolon (*in vivo*) | $^{31}$P NMR | | + | + | | | | | | | | | | 45 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Tuber | IEC | 5 | 11 | 11 | 2 | 2 | 3 | | | 6 | 2 | 4 | 2576 |
| 1 | Tuber | Lumin. | 22.2 | 8.2 | 23.0 | | | | | | | | | 2575 |
| *Hemerocallis* hybrid (Daylily) | | | | | | | | | | | | | | |
| 1 | Flower petal[q] (*incl. CDP) | TLC/TLC | 3.8 | 8.7 | 43.4 | | 2.9* | 6.8 (incl. CTP) | | | 3.5 | 1.9 | 9.3 | 266 |
| *Heracleum mantegazzianum* Somm. and Lev. (Giant Hogweed) | | | | | | | | | | | | | | |
| 1 | Phloem[d] | Enzym. | | | 650 | | | | | | | | | 2444 |
| 1 | Xylem[d] | Enzym. | | | 360 | | | | | | | | | 2444 |
| 1 | Parenchyma[d] | Enzym. | | | 240 | | | | | | | | | 2444 |
| *Heracleum sosnowskii* Mandan (Cow Parsnip) | | | | | | | | | | | | | | |
| 1 | Vascular bundle, phloem | PC/PC | 133 | 92 | 81 | 14 | 26 (incl. GTP) | | 16 | 22 | 268 | 199* | 64 | 2577 |
| 1 | –, xylem (*incl. UDPX) | PC/PC | 51 | 24 | 50 | Trace | 20 (incl. GTP) | | 0 | 8 | 156 | 159* | 34 | 2577 |
| *Hevea brasiliensis* Müll. (Pará Rubber Tree) | | | | | | | | | | | | | | |
| 1 | Latex[d] | PE | | 74 | 15 | | | | 39 | 48 | | 30 | | 2578 |
| 1 | Latex[b] | Lumin. | 26 | 30 | 77 | | | | | | | | | 2579 |
| *Hibiscus cannabinus* L. (Kenaf) | | | | | | | | | | | | | | |
| 1 | Leaf[a] | | | | + | | | | | | | | | 2580 |
| *Hippophaë salicifolia* D. Don (Willow-Leaved Sea Buckthorn) | | | | | | | | | | | | | | |
| 1 | Phloem exudate[b] | Enzym. | | | 360 | | | | | | | | | 2444 |
| *Hordeum distichon* Alef. (Two-Rowed Barley) | | | | | | | | | | | | | | |
| 1 | Seed[a] | PC/PE | | | | | | | | | + | | | 2512 |
| – ssp. *nutans* (Rode) Alef. | | | | | | | | | | | | | | |
| 3 | Leaf | PC | + | + | + | + | | + | + | | + | | + | 2581 |
| 2 | Etiolated seedling | PC | + | + | + | + | | + | + | | + | | + | 2581 |
| 1 | 1-day seedling, cotyledon[d,g] | Enzym. | | 45 | 37.5 | | | | | | | | | 267 |
| 1 | Crown[o] | Lumin. | 0.18 | 1.90 | 2.19 | | | | | | | | | 2582 |
| *Hordeum hexastichon* Alef. ssp. *parallelum* Körn (Six-Rowed Barley) | | | | | | | | | | | | | | |
| 1 | Leaf | PC | + | + | + | + | | + | + | | + | | + | 2581 |

*nmol/g fwb unless stated otherwise. [a]Taken from the abstract. [b]µmol/L. [c]µg/plant part. [d]Dry weight basis. [e]nmol/$10^7$ cells. [f]ppm. [g]nmol/plant part. [h]nmol/mg insoluble polysaccharide. [i]µg/g. [j]µg/mL. [k]nmol/$10^6$ protoplasts. [l]µmol/$m^2$. [m]µmol/g. [n]µmol/$10^7$ cells. [o]nmol/mg protein. [p]nmol/mg chlorophyll. [q]Percentage of total free nucleotides. [r]m*M*. [s]mg/g. [t]Percentage P dwb. [u]Total extinction/callus (plant part). [v]counts per minute × $10^3$.

*Continued*

**Table 5-2** Ribonucleotides in Plants*—cont'd

| No. | Plant part | Method | AMP | ADP | ATP | GMP | GDP | GTP | CMP | CDP | CTP | UMP | UDP | UTP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Hordeum vulgare* L. (Barley) | | | | | | | | | | | | | | | |
| 1 | Seed[a] | PC/PE | | | | | | | | | | + | | | 2512 |
| 1 | Seed | IEC | 33 | 43 | 40 | 0 | 8 | 7 | 0 | 3 | 5 | 37 | 29 | 18 | 2471 |
| 2 | Grain, dehusked[g] | Enzym. | | | | | | | | | | | 2.5-3.5 | 4.0-7.5 | 502 |
| 14 | Seed, spring[g] | Lumin. | | | 0.057-0.083 | | | | | | | | | | 2583 |
| 13 | Seed, winter[g] | Lumin. | | | 0.057-0.087 | | | | | | | | | | 2583 |
| 1 | Leaf[i] | Enzym. | 6.4 | 12.1 | 12.5 | | | | | | | | | | 2584 |
| 1 | Leaf | HPLC | 20.4 | 26.3 | 26.8 | | | | | | | | | | 2585 |
| 1 | Leaf | Lumin. | | | 245 | | | | | | | | | | 524 |
| 1 | Shoot[d,i] | Lumin. | | | 103.8 | | | | | | | | | | 2469 |
| 1 | Root | PC/PC | | + | + | | | | | | | | | | 2586 |
| 1 | 20-day root | HPLC | | 81 | 166 | | 44 | 19 | | | 82 | | 57 | | 2587 |
| 1 | Root | Lumin. | 520 | 773 | 1385 | | | | | | | | | | 2588 |
| 1 | Root tip (*in vivo*) | $^{31}$P NMR | | | + | | | | | | | | | | 2589 |
| *Hygrohypnum luridum* (Hedw.) Jenn. (Hygrohypnum Moss) | | | | | | | | | | | | | | | |
| 1 | Whole moss, hydrated | Lumin. | | | 570 | | | | | | | | | | 2590 |
| *Ilex paraguariensis* St. Hil. (Maté) | | | | | | | | | | | | | | | |
| 1 | Leaf | HPLC | 71 | 110 | 121 | 9 | 21 | 30 | | | | | | | 2591 |
| *Impatiens balsamina* L. (Garden Balsam) | | | | | | | | | | | | | | | |
| 1 | Root tip[d,m] | Enzym. | | | 13.3 | | | | | | | | | | 497 |
| *Ipomoea batatas* (L.) Lam. (Sweet Potato) | | | | | | | | | | | | | | | |
| 1 | Tuber | HPLC | 6 | | | n.d. | | | 100 | | | 34 | | | 2468 |
| 1 | Root | IEC | 43.6 | 2.2 | 35.9 | | | | | | | 18.5 | | 8.4 | 2592 |
| 1 | Root | IEC | 12.3 | 68.9 | 131 | | | | | | | | | | 2593 |
| *Juglans regia* L. ssp. *orientis* Sarg. (English Walnut) | | | | | | | | | | | | | | | |
| 1 | Bark[d] | Lumin. | | | 210 | | | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 117 | | | | | | | | | | 2487 |
| *Juncus roemerianus* Scheele (Needlegrass Rush) | | | | | | | | | | | | | | | |
| 1 | Stem base[d,i] | Lumin. | + | + | 40.0 | | | | | | | | | | 2594 |
| 1 | Root[d,i] | Lumin. | + | + | 1.3 | | | | | | | | | | 2594 |
| 1 | Rhizome[d,i] | Lumin. | + | + | 7.5 | | | | | | | | | | 2594 |
| 1 | –, less bark[d,i] | Lumin. | + | + | 22.4 | | | | | | | | | | 2594 |
| 1 | –, bark[d,i] | Lumin. | + | + | 6.8 | | | | | | | | | | 2594 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, tip[d,i] | Lumin. | + | + | 99.9 | | | | | | | | | 2594 |
| *Kalanchoë blossfeldiana* v. Poelln. (Flaming Katy) | | | | | | | | | | | | | | |
| 1 | Seed[d,g] | Lumin. | 880 | 310 | 110 | | | | | | | | | 2595 |
| 1 | Leaf | Lumin. | | | 32 | | | | | | | | | 2596 |
| *Kalanchoë daigremontiana* Ham. and Perr. (Devil's Backbone) | | | | | | | | | | | | | | |
| 1 | Leaf | Lumin. | 14 | 14 | 27 | | | | | | | | | 2596 |
| *Kalanchoë tubiflora* (Harv.) Hamet (Chandelier Plant) | | | | | | | | | | | | | | |
| 1 | Phyllodium[d] | Lumin. | | | 230 | | | | | | | | | 2597 |
| *Koelreuteria paniculata* Laxm. (Golden Rain Tree) | | | | | | | | | | | | | | |
| 1 | Phloem exudate[b] | Enzym. | | | 220 | | | | | | | | | 2444 |
| *Lactuca sativa* L. (Lettuce) | | | | | | | | | | | | | | |
| 1 | Seed | HPLC | + | + | + | + | + | + | | + | | | + | 2598 |
| 2 | Seed[d] | Lumin. | 164-219 | 74-76 | 10 | | | | | | | | | 2599 |
| 1 | Seed[g] | Lumin. | | | 0.24 | | | | | | | | | 2454 |
| 3 | Seed, imbibed | Lumin. | | | 609-698 | | | | | | | | | 2600 |
| 1 | Leaf | IEC | 27 | | | Trace | | | | | 16 | | | 2456 |
| 1 | Leaf[i] | IEC | 5 | 5 | 6 | 7 | | | 2 | | 6 | | | 2496 |
| 1 | Sprout (extract) | $^{31}$P NMR | + | | | | | | | | | | | 48 |
| *Larix decidua* Mill. (European Larch) | | | | | | | | | | | | | | |
| 1 | Cambium | IEC | 25.3 | 4.7 | 2.8 | 3.9 | 1.7 | 0.8 | | | 19.3 | 4.4 | 2.6 | 2601 |
| 1 | Young xylem | IEC | 3.3 | 0.2 | | 0.4 | | | | | 1.7 | 0.1 | | 2601 |
| *Leleba oldhamii* (Munro) Nakai (Summer Bamboo) | | | | | | | | | | | | | | |
| 1 | Desheathed shoot | IEC | 67.5 | 8.8 | 23.8 | 7.5 | | | | | 12.6 | 5.0 | | 2602 |
| *Lemna gibba* L. (Gibbous Duckweed) | | | | | | | | | | | | | | |
| 1 | Whole plant | Enzym. | 13 | 47 | 99 (lumin.) | | | | | | | | | 2603 |
| *Lemna paucicostata* Hegelm. (Lesser Duckweed) | | | | | | | | | | | | | | |
| 1 | Frond | Lumin. | | | 156 | | | | | | | | | 2604 |
| *Lens culinaris* Medik. (Lentil) | | | | | | | | | | | | | | |
| 1 | Sprout | HPLC | + | | | + | | | | | + | | | 2605 |

*nmol/g fwb unless stated otherwise. [a]Taken from the abstract. [b]µmol/L. [c]µg/plant part. [d]Dry weight basis. [e]nmol/$10^7$ cells. [f]ppm. [g]nmol/plant part. [h]nmol/mg insoluble polysaccharide. [i]µg/g. [j]µg/mL. [k]nmol/$10^6$ protoplasts. [l]µmol/$m^2$. [m]µmol/g. [n]µmol/$10^7$ cells. [o]nmol/mg protein. [p]nmol/mg chlorophyll. [q]Percentage of total free nucleotides. [r]m*M*. [s]mg/g. [t]Percentage P dwb. [u]Total extinction/callus (plant part). [v]counts per minute × $10^3$.

*Continued*

**Table 5-2** Ribonucleotides in Plants*—cont'd

| No. | Plant part | Method | AMP | ADP | ATP | GMP | GDP | GTP | CMP | CDP | CTP | UMP | UDP | UTP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Lilium henryi* Bak. (Lily) | | | | | | | | | | | | | | | |
| 1 | Pollen | PC/PC | + | | | + | | | + | | | | | | 2606 |
| *Linum usitatissimum* L. (Flax, Linseed) | | | | | | | | | | | | | | | |
| 1 | Seed | IEC | + | | | + | | | + | | | + | | | 2607 |
| 1 | Seed[a] | Lumin. | 181.0 (incl. ADP and ATP) | | | | | | | | | | | | 2495 |
| 10 | Seed | HPLC | 71.1-73.4 | 14.5-25.3 | 7.6-227.4 | | | | | | | | | | 2608 |
| *Liriodendron tulipifera* L. (Tulip Tree) | | | | | | | | | | | | | | | |
| 1 | Leaf | IEC | 13.0 | | | 16.4 | | | 0.5 | | | 6.1 | 4.9 | 7.4 | 2543 |
| *Lolium perenne* L. (Perennial Ryegrass) | | | | | | | | | | | | | | | |
| 1 | Leaf | Lumin. | | | 160 | | | | | | | | | | 2609 |
| *Lotus corniculatus* L. (Birdsfoot Trefoil) | | | | | | | | | | | | | | | |
| 1 | Root[b] | HPLC | | 25 | 47 | | | | | | | | | | 508 |
| *Lupinus luteus* L. (Yellow Lupine) | | | | | | | | | | | | | | | |
| 1 | Seed | IEC | ++ | ++ | + | + | | | | | | + | | | 2437 |
| 1 | –, axis | Lumin. | | | 100 | | | | | | | | | | 2610 |
| 1 | –, cotyledon | Lumin. | | | 10 | | | | | | | | | | 2610 |
| *Lycium chinense* Mill. (Box Thorn) | | | | | | | | | | | | | | | |
| 1 | Leaf | IEC | | | | | | | + | | | + | | | 2611 |
| *Lycopersicon esculentum* Mill. (Tomato) | | | | | | | | | | | | | | | |
| 1 | Leaf[d] | PC/PC | 105 | 340 | 615 | | 30 | 150 | | | 250 | 45 | 70 | 400 | 2612 |
| 1 | Leaf | IEC | 20.7 | 69.1 | 143.8 | | 11.7 | 27.5 | | | 8.2 | 15.9 | | 9.5 | 2613 |
| 2 | Fruit, immature, whole | PC/PE | 2.7 | 3.2 | 1.6-2.2 | 0.2-0.9 | 0.5-0.8 | | | | | 0.2 | 0.2-0.5 | | 2614 |
| 1 | Fruit | IEC | 300 | | | | | | 14 | | | 68 | | | 2456 |
| 1 | Fruit[m] | IEC | 11.5 | 4.8 | 38.4 | | | | | | | 27 | | 75 | 2615 |
| 1 | Fruit[i] | Enzym. | 0.5 | 4 | 16 | | | | | | | | | | 2616 |
| 1 | Fruit, pericarp[b] | HPLC | 100 | | | | | | | | | | | | 2617 |
| 1 | –, locular | HPLC | 40 | | | | | | | | | | | | 2617 |
| 1 | Seedling | IEC | | + | + | | | | | | | | | | 2527 |
| 1 | Root tip | HPLC | 11.2 | 3.5 | 6.5 | 6.0 | 1.5 | 2.9 | 31.0 | 2.7 | 2.7 | 55.0 | 3.4 | 2.9 | 2618 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Machilus thunbergii* Sieb. and Zucc. | | | | | | | | | | | | | | | |
| 1 | Seed[a,d] | | + | | >20 | | | | | | | | | | 2534 |
| 1 | Seed[d] | Lumin. | 13.3 | 34.6 | 55.0 | | | | | | | | | | 2619 |
| *Magnolia grandiflora* L. (Southern Magnolia) | | | | | | | | | | | | | | | |
| 1 | Leaf | IEC | 27.5 | 5.1 | | 16.2 | 10.0 | 1.5 | 6.2 | | | 12.1 | 8.1 | | 2543 |
| *Magnolia kobus* DC ssp. *borealis* Sarg. | | | | | | | | | | | | | | | |
| 1 | Bark[d] | Lumin. | | | 466 | | | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 58 | | | | | | | | | | 2487 |
| *Malus baccata* (L.) Borkh. (Siberian Crabapple) | | | | | | | | | | | | | | | |
| 1 | Root | Lumin. | | | 17.42 | | | | | | | | | | 2620 |
| *Malus domestica* Borkh. (Apple) | | | | | | | | | | | | | | | |
| 1 | Seed, embryonic axis[g] | Lumin. | | | 0.216 | | | | (Other NTP 0.115) | | | | | | 2621 |
| 1 | –, cotyledon[g] | Lumin. | | | 1.254 | | | | (Other NTP 0.655) | | | | | | 2621 |
| 1 | Leaf | IEC | + | + | + | | + | + | | | + | | | | 2622 |
| 3 | Phloem exudate[f] | HPLC | 1-2 | 4-30 | 2-14 | 1-2 | 1-3 | 2-5 | 3-7 | 1-2 | 1-2 | 6-24 | 4-14 | 1 | 2623 |
| 1 | Fruit[i] | Lumin. | | | 2000 | | | | | | | | | | 2467 |
| 1 | Bark[d] | Lumin. | | | 154 | | | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 42 | | | | | | | | | | 2487 |
| *Malus sylvestris* (L.) Mill. (Crabapple) | | | | | | | | | | | | | | | |
| 1 | Stem, phloem tissue | PC/PC | | + | + | | | | | | | | | | 227 |
| *Malus xiaojinensis* Cheng and Jiang | | | | | | | | | | | | | | | |
| 1 | Root | Lumin. | | | 9.98 | | | | | | | | | | 2620 |
| *Medicago sativa* L. (Alfalfa) | | | | | | | | | | | | | | | |
| 1 | Shoot | PC/PC | + | + | + | | | | | | | | | | 280 |
| 1 | Root | PC/PC | + | + | + | | | | | | | | | | 280 |
| 1 | Root[d] | HPLC | | 17 | 31 | | | | | | | | | | 508 |
| *Metasequoia glyptostroboides* Hu and Cheng (Dawn Redwood) | | | | | | | | | | | | | | | |
| 1 | Bark[d] | Lumin. | | | 60 | | | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 31 | | | | | | | | | | 2487 |
| *Michelia compressa* (Maxim.) Sargent | | | | | | | | | | | | | | | |
| 1 | Seed[a,d] | | + | | <10 | | | | | | | | | | 2534 |

*nmol/g fwb unless stated otherwise. [a]Taken from the abstract. [b]μmol/L. [c]μg/plant part. [d]Dry weight basis. [e]nmol/$10^7$ cells. [f]ppm. [g]nmol/plant part. [h]nmol/mg insoluble polysaccharide. [i]μg/g. [j]μg/mL. [k]nmol/$10^6$ protoplasts. [l]μmol/$m^2$. [m]μmol/g. [n]μmol/$10^7$ cells. [o]nmol/mg protein. [p]nmol/mg chlorophyll. [q]Percentage of total free nucleotides. [r]m*M*. [s]mg/g. [t]Percentage P dwb. [u]Total extinction/callus (plant part). [v]counts per minute × $10^3$.

*Continued*

**Table 5-2** Ribonucleotides in Plants*—cont'd

| No. | Plant part | Method | AMP | ADP | ATP | GMP | GDP | GTP | CMP | CDP | CTP | UMP | UDP | UTP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Morus alba* L. (White Mulberry) | | | | | | | | | | | | | | | |
| 1 | Shoot, debarked | Lumin. | 5 | 8 | 4 | | | | | | | | | | 2624 |
| 1 | –, bark | Lumin. | 12 | 25 | 10 | | | | | | | | | | 2624 |
| *Morus bombycis* Koidz. | | | | | | | | | | | | | | | |
| 1 | Bark[d] | Lumin. | | | 213 | | | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 86 | | | | | | | | | | 2487 |
| *Mucuna pruriens* (L.) DC (Cowitch Bean) | | | | | | | | | | | | | | | |
| 1 | Leaf[f] | Ennzym. | 20 | 20 | | | | | | | | | | | 282 |
| *Musa* × *paradisiaca* L. (Banana) | | | | | | | | | | | | | | | |
| 1 | Fruit | Enzym. | | | 113 | | | | | | | | | | 2625 |
| *Neolitsea parvigemma* (Hayata) Kaneh. and Sas. | | | | | | | | | | | | | | | |
| 1 | Seed[a,d] | | + | | >20 | | | | | | | | | | 2534 |
| *Nicotiana glutinosa* L. (Tobacco) | | | | | | | | | | | | | | | |
| 1 | Leaf[d] | Lumin. | | 231 | 223 | | | | | | | | | | 2626 |
| *Nicotiana tabacum* L. (Tobacco) | | | | | | | | | | | | | | | |
| 1 | Leaf | PC/PC | | + | + | | | | | | | | | | 2627 |
| 1 | Leaf | HPLC | 9.9 | 15.9 | 28 | 0.5 | 2.4 | 4.7 | | 3.8 | 6.0 | 3.3 | 4.4 | 11.6 | 2440 |
| | | | and variation from top (apex) leaf to lowest (senescent) leaf of a single plant | | | | | | | | | | | | 2628 |
| 1 | Leaf | Enzym. | 14.4 | 30.8 | 71.2 | | | | | | | | | | 287 |
| 1 | Pollen grain (*in vivo*) | $^{31}$P NMR | | | + | | | | | | | | | | 2563 |
| 1 | Root | PC/PC | | + | + | | | | | | | | | | 2627 |
| 1 | Root | HPLC | 1.0 | 7.8 | 15 | 0.4 | 0.5 | 2.3 | | | | 4.9 | 1.0 | 6.7 | 2440 |
| 1 | Cell suspension culture | HPLC | 3.9 | 13.5 | 85 | | 3.2 | 15.4 | | 1.2 | 3.2 | 19.1 | 12.2 | 26 | 2440 |
| 1 | Cell suspension culture (extract or *in vivo*) | $^{31}$P NMR | | + | + | | | | | | | | | | 2629 |
| 1 | Callus tissue[d] | TLC/TLC | | | 780 | | | 150 | | | 270 | | | 170 | 2434 |
| 1 | Callus culture | Lumin. | 20 | 50 | 155 | | | | | | | | | | 2630 |
| 1 | Seed | Enzym. | 20 | 140 | 370 | | | | | | | | | | 2631 |
| 1 | Seed | Lumin. | | | 0 | | | | | | | | | | 2632 |
| 1 | Seed[d] | Lumin. | 60.9 (incl. ADP and ATP) | | | | | | | | | | | | 2495 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Oryza sativa* L. (Rice) | | | | | | | | | | | | | | |
| 1 | Seed[a] | Fluorometric | | | + | | | | | | | | | 2491 |
| 1 | Kernel | IEC | 113.04 | 68.46 | 35.18 | | 2.96 | | 2.16 | 1.36 | 6.64 | 44.58 | 11.98 | 9.88 | 2633 |
| 1 | Seed embryo | Enzym. | 44 | 107 | 76 | | | | | | | | | | 2634 |
| 1 | Ripening grain, 10 daf | IEC | 30 | 72 | 84 | 31 | 7 | 8 | | | | 67 | 67 | 50 | 2635 |
| 5 | Leaf[c] | Lumin. | | | 13.8-21.6 | | | | | | | | | | 2559 |
| 1 | Leaf and culm | IEC | ++ | | | | | | | | | + | + | + | 2636 |
| 1 | Leaf sheath phloem sap[r] | HPLC | Trace | 0.31 | 1.63 | | | 0.21 | | | 0.08 | | | 0.27 | 2637 |
| 1 | Upper internode phloem sap[r] | HPLC | Trace | 0.27 | 1.76 | | | 0.22 | | | 0.04 | | | 0.10 | 2637 |
| 1 | Shoot | Lumin. | | | 130 | | | | | | | | | | 2638 |
| 1 | Shoot (*in vivo*) | $^{31}$P NMR | | | | NTP | | | | | | | | | 2638 |
| 1 | Root | HPLC | 350 | 1660 | 2660 | | | | | | | | | | 2639 |
| 1 | Seedling, root[a] | IEC | + | + | + | | | | | | | | | | 2640 |
| 1 | Cell suspension culture | IEC | 48.4 | 66.1 | 63.1* | 14.9 | 50.0 | | *Incl. UDP | | | 78.3 | 32.0 | 7.4 | 2641 |
| *Panicum hemitomon* Schult. | | | | | | | | | | | | | | | |
| 1 | Root[d] | Lumin. | 72 | 38 | 465 | | | | | | | | | | 2642 |
| *Panicum miliaceum* L. (Proso Millet) | | | | | | | | | | | | | | | |
| 1 | Leaf mesophyll chloroplast[p] | Lumin. | | | 4.3 | | | | | | | | | | 2643 |
| *Persea americana* Mill. (Avocado) | | | | | | | | | | | | | | | |
| 1 | Fruit[s] | HPLC | | 80 | 80 | | | | | | | | | | 515 |
| 1 | Fruit (*in vivo*) | $^{31}$P NMR | | + | + | | | | | | | | | | 515 |
| *Phacelia tanacetifolia* Benth. (Fiddleneck) | | | | | | | | | | | | | | | |
| 1 | Seed[g] | Lumin. | | | 0.019 | | | | | | | | | | 2644 |
| 1 | Sprout (*in vivo*) | $^{31}$P NMR | | | | | NDP, NTP | | | | | | | | 2644 |
| *Pharbitis nil* Choisy (Morning Glory) | | | | | | | | | | | | | | | |
| 1 | Seedling, hypocotyl[d] | Lumin. | 190 | 700 | 2030 | | | | | | | | | | 2645 |
| 1 | –, plumule[d] | Lumin. | | | 4000 | | | | | | | | | | 2645 |
| 1 | –, cotyledon | Lumin. | | | 5 | | | | | | | | | | 2646 |
| 1 | –, apex | Lumin. | | | 150 | | | | | | | | | | 2646 |

*nmol/g fwb unless stated otherwise. [a]Taken from the abstract. [b]μmol/L. [c]μg/plant part. [d]Dry weight basis. [e]nmol/$10^7$ cells. [f]ppm. [g]nmol/plant part. [h]nmol/mg insoluble polysaccharide. [i]μg/g. [j]μg/mL. [k]nmol/$10^6$ protoplasts. [l]μmol/$m^2$. [m]μmol/g. [n]μmol/$10^7$ cells. [o]nmol/mg protein. [p]nmol/mg chlorophyll. [q]Percentage of total free nucleotides. [r]m*M*. [s]mg/g. [t]Percentage P dwb. [u]Total extinction/callus (plant part). [v]counts per minute × $10^3$.

*Continued*

**Table 5-2** Ribonucleotides in Plants*—cont'd

| No. | Plant part | Method | AMP | ADP | ATP | GMP | GDP | GTP | CMP | CDP | CTP | UMP | UDP | UTP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Phaseolus vulgaris* L. (Bush Bean) | | | | | | | | | | | | | | | |
| 1 | Seed | IEC | ++ | ++ | + | + | | | | | | + | | | 2437 |
| 1 | Seed[d] | HPLC | 1630 | | | 1040 | | | | | | | | | 2647 |
| 1 | Seed | Enzym. | 20 | 140 | 370 | | | | | | | | | | 2631 |
| 1 | Seed[i] | Lumin. | | | 21.0 | | | | | | | | | | 2547 |
| 1 | Embryo[d,i] | IEC | 8.4 | | | 1.7 | | | n.d. | | | n.d. | | | 2648 |
| 1 | Green bean | IEC | 53 | | | | | | 26 | | | 81 | | | 2456 |
| 1 | Leaf[q] | PC/PC | | | | | | | | 1.5 | 0.9 | 8.3 | 10.5 | 4.2 | 12 |
| 1 | Leaf | IEC | 210 | 190 | 140 | | | | | | | | | | 22 |
| 1 | Leaf | IEC | 19.9 | 54.2 | 77.5 | | 8.8 | 15.8 | | | 4.3 | 8.6 | | 5.4 | 2649 |
| 1 | Leaf[d] | Lumin. | 890 | 600 | 400 | | | | | | | | | | 2546 |
| 1 | Etiolated leaf[g] | IEC | 3.3 | | 2.7 | 0.9 | 0.9 | | 3.4 | | | 3.5 | | | 2650 |
| 1 | Leaf | HPLC | 22 | | | n.d. | | | n.d. | | | 70 | | | 2468 |
| 1 | Leaf, mature | HPLC[2651] | 59 | 100 | 53 | | 14 | 10 | | | 3 | 17 | 24 | 18 | 2652 |
| 1 | –, young | HPLC | 50 | 160 | 162 | | 41 | 49 | | | 20 | 66 | 33 | 55 | 2652 |
| 1 | Leaf, petiole | IEC | 1 | 3 | 33 | – | | 6 | 1 | | 1 | 0.5 | – | 9 | 2653 |
| 1 | –, laminae | IEC | 12 | 18 | 69 | 7 | | 8 | | | | 15 | | 14 | 2653 |
| 1 | Stem | IEC | 22 | 40 | 56.5 | | | | | | | 75 | 43 | | 2654 |
| 1 | Fruit, pericarp | IEC | 17 | 11 | 69 | | | | | | | 22 | | 54 | 520 |
| 1 | Whole seedling | Lumin. | 21.5 | 24.0 | 81.0 | | | | | | | | | | 2655 |
| 1 | Seedling | IEC | 25.0 | 25.0 | 80.0 | 10.5 | | 18.0 | 4.5 | | 6.5 | 19.5 | 8.0 | 21.0 | 2656 |
| 1 | –, leaf | IEC | 30 | 60 | 280 | 0.0 | | 40 | | | | 25 | | 60 | 2657 |
| 1 | –, leaf | Lumin. | | | 320 | | | | | | | | | | 2474 |
| 1 | –, root | IEC | 15 | 22 | 110 | 10 | | 140 | | | | 15 | | 47 | 2657 |
| 1 | –, root | Lumin. | 5 | 9 | 56 | | | | | | | | | | 2658 |
| *Phaseolus vulgaris* L. ssp. *napus* (Dwarf Common Bean) | | | | | | | | | | | | | | | |
| 1 | Leaf[d,i] | Lumin. | | | 134 | | | | | | | | | | 2659 |
| *Phellodendron wilsonii* Hayata and Kaneh. | | | | | | | | | | | | | | | |
| 1 | Seed[a,d] | | + | | <10 | | | | | | | | | | 2534 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Phragmites australis* (Cav.) Steud. (Reed) | | | | | | | | | | | | | | |
| 1 | Root | | 20.8 (incl. ADP and ATP) | | | | | | | | | | | 2660 |
| 1 | Rhizome | | 51.2 (incl ADP and ATP) | | | | | | | | | | | 2660 |
| *Phyllostachys bambusoides* Sieb. and Zucc. (Timber Bamboo) | | | | | | | | | | | | | | |
| 1 | Sap[a] | | + | | | + | | | + | | | + | | 2451 |
| *Phyllostachys nigra* (Lodd ex Lindl.) Munro (Black Bamboo) | | | | | | | | | | | | | | |
| 1 | Sap[a] | | + | | | + | | | + | | | + | | 2451 |
| *Phyllostachys pubescens* Mazel ex Houz. (Moso Bamboo) | | | | | | | | | | | | | | |
| 1 | Desheathed shoot | IEC | 58.4 | 13.6 | 4.8 | 12.4 | 2.4 | | | | | 15.6 | 12.8 | 2661 |
| 1 | Sap[a] | | + | | | + | | | + | | | + | | 2451 |
| *Picea abies* (L.) Karst. (Norway Spruce) | | | | | | | | | | | | | | |
| 1 | Seed, endosperm[d] | Enzym. | | + | 100 | | | | | | | | | 523 |
| 1 | –, embryo[d] | Enzym. | | + | 430 | | | | | | | | | 523 |
| 1 | Needle (leaf)[d] | HPLC | 5.8 | 61.0 | 54.4 | | | | | | | | | 2662 |
| 1 | Needle (leaf)[d] | Lumin. | | 65 | 321 | | | | | | | | | 2663 |
| *Pinus banksiana* Lamb. (Jack Pine) | | | | | | | | | | | | | | |
| 1 | Seed[g] | Lumin. | | | 5.4 | | | | | | | | | 2664 |
| 1 | 11-day seedling[q] | IEC | 57.0 | 14.0 | 11.0 | 1.0 | 2.0 | 1.0 | 4.0 | 1.0 | 0.6 | 1.0 | 1.0 | 0.4 | 2665 |
| *Pinus contorta* × *Pinus banksiana* (Lodgepole-Jack Pine) | | | | | | | | | | | | | | |
| 1 | Needle (leaf)[d] | Lumin. | | | 658 | | | | | | | | | 2666 |
| *Pinus koraiensis* Sieb. and Zucc. (Korean Pine) | | | | | | | | | | | | | | |
| 1 | Bark[d] | Lumin. | | | 240 | | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 72 | | | | | | | | | 2487 |
| *Pinus lambertiana* Dougl. (Sugar Pine) | | | | | | | | | | | | | | |
| 1 | Seed[d] | Lumin. | | | 47 | | | | | | | | | 2667 |
| 1 | –, embryo | Lumin. | | | 370 | | | | | | | | | 2668 |
| 1 | –, megagametophyte | Lumin. | | | 200 | | | | | | | | | 2668 |
| *Pinus mugo* Turra (Mugo Pine) | | | | | | | | | | | | | | |
| 1 | Pollen[d] | TLC/TLC | | | 1350 | | | 370 | | | 310 | | | 700 | 2434 |
| 1 | Pollen | Lumin. | | | 300 | | | | | | | | | | 2669 |

*nmol/g fwb unless stated otherwise. [a]Taken from the abstract. [b]μmol/L. [c]μg/plant part. [d]Dry weight basis. [e]nmol/$10^7$ cells. [f]ppm. [g]nmol/plant part. [h]nmol/mg insoluble polysaccharide. [i]μg/g. [j]μg/mL. [k]nmol/$10^6$ protoplasts. [l]μmol/$m^2$. [m]μmol/g. [n]μmol/$10^7$ cells. [o]nmol/mg protein. [p]nmol/mg chlorophyll. [q]Percentage of total free nucleotides. [r]m*M*. [s]mg/g. [t]Percentage P dwb. [u]Total extinction/callus (plant part). [v]counts per minute × $10^3$.

*Continued*

**Table 5-2** Ribonucleotides in Plants*—cont'd

| No. | Plant part | Method | AMP | ADP | ATP | GMP | GDP | GTP | CMP | CDP | CTP | UMP | UDP | UTP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pinus ponderosa* Laws. (Ponderosa Pine) | | | | | | | | | | | | | | | |
| 1 | Mature seed, embryo[g] | Lumin. | 0.130 | 0.350 | 0.060 | | | | | | | | | | 2670 |
| 1 | –, gametophyte[g] | Lumin. | 0.600 | 0.480 | 0.060 | | | | | | | | | | 2670 |
| *Pinus resinosa* Ait. (Red Pine) | | | | | | | | | | | | | | | |
| 1 | Ovule, embryo | Lumin. | | | 0.72 | | | | | | | | | | 2671 |
| 1 | –, gametophyte | Lumin. | | | 0.10 | | | | | | | | | | 2671 |
| *Pinus strobus* L. (Eastern White Pine) | | | | | | | | | | | | | | | |
| 1 | Bark [d] | Lumin. | | | 101 | | | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 29 | | | | | | | | | | 2487 |
| *Pinus sylvestris* L. (Scotch Pine) | | | | | | | | | | | | | | | |
| 1 | Seed, endosperm[d] | Enzym. | | + | 100 | | | | | | | | | | 523 |
| 1 | –, embryo[d] | Enzym. | | + | 250 | | | | | | | | | | 523 |
| 1 | Needle (leaf)[d] | Lumin. | 37 | 72 | 176 | | | | | | | | | | 2672 |
| 1 | Root | Lumin. | 6 | 34 | 101 | | | | | | | | | | 2673 |
| *Pistacia mutica* Fisch. and Mey (Mt. Atlas Mastic Tree) | | | | | | | | | | | | | | | |
| 1 | Leaf[i] | Lumin. | | | 6.0 | | | | | | | | | | 2674 |
| *Pisum sativum* L. (Pea) | | | | | | | | | | | | | | | |
| 1 | Mature seed | PC/PC | | ++ | +++ | | | + | | | | | | + | 52 |
| 1 | Mature seed | Enzym. | | 198 | 374 | | | | | | | | | | 52 |
| 1 | Seed | Enzym. | 21 | 102 | 286 | | | | | | | | | | 296 |
| 2 | Seed embryo | Enzym. | | | | | | | | | | | | 175-351 | 295 |
| 1 | Seed[i] | PC/PC | 2.7 | 38.0 | 8.1 | | | | | | | | | | 2675 |
| 1 | Seed[d] | Lumin. | 1000.0 (incl. ADP and ATP) | | | | | | | | | | | | 2495 |
| 1 | Leaf[i] | PC/PC | 37.9 | 149.0 | 131.4 | | | | | | | | | | 2675 |
| 1 | Leaf[i] | Enzym. | 5.25 | 17.8 | 16.5 | | | | | | | | | | 2584 |
| 1 | Stem[i] | PC/PC | 64.6 | 182.0 | 182.0 | | | | | | | | | | 2675 |
| 1 | Seed | IEC | 447 | 218 | 86 | 13 | | | | Trace | | 57 | | | 2437 |
| 1 | Seed | HPLC | 11 | 116 | 133 | 9 | 20 | 27 | n.d. | n.d. | 39 | 96 | 86 | 289 | 2441 |
| 1 | Immature seed with pod | IEC | 55 | | | | | | Trace | | | 40 | | | 2456 |
| 1 | Seed coat | Enzym. | | | | | | | | | | | | 272 | 2676 |
| 1 | Leaf chloroplast | PC/PC | + | + | + | | | | | | | | | | 2677 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 14-day shoot[d] | PC | | | | | | 1708 | | + | | | 2678 |
| 1 | 2-day cotyledon | Enzym. | 70 | 30 | 230 | | | | | | | | 2679 |
| 1 | Seedling, cotyledon | Enzym. | | | | | | | | | 32 | 67 | 527 |
| 1 | Shoot | PC/PC | + | + | + | | + | | | | + | + | 2680 |
| 1 | Whole seedling | PC/PC | | + | + | | | | | + | + | + | 2681 |
| 1 | Whole plant | PE | | | 15 | | | | | | | | 2682 |
| 1 | Root[i] | PC/PC | 42.2 | 105.5 | 85.2 | | | | | | | | 2675 |
| 1 | Root | PC/PC | + | + | + | | + | | | | + | + | 2680 |
| 1 | Root | IEC | + | + | + | | | | | + | + | | 2654 |
| 1 | Root[d] | CC (cellulose) | 1490 | 790 | 4400 | | 200 | | 570 | | | 860 | 2683 |
| 1 | Root tip | Enzym. | 8.65 | 23.68 | 88.1 | | | | | | | | 2684 |
| 1 | Root tip (*in vivo*) | $^{31}$P NMR | | | | NDP, NTP | | | | | | | 526 |
| *Platanus occidentalis* L. (Eastern Sycamore) | | | | | | | | | | | | | |
| 1 | Bark[d] | Lumin. | | | 157 | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 81 | | | | | | | | 2487 |
| *Poa annua* L. (Annual Bluegrass) | | | | | | | | | | | | | |
| 1 | Root[t] | HPLC | | | $10^{-4}$ | | | | | | | | 696 |
| *Podocarpus macrophyllus* (Thunb.) Sweet (Yew Plum Pine) | | | | | | | | | | | | | |
| 1 | Seed[a,d] | | + | | >20 | | | | | | | | 2534 |
| *Populus gelrica* (Houtz.) Houtz. | | | | | | | | | | | | | |
| 1 | Twig, living bark[d] | Lumin. | 23.5 | 14.1 | 84.3 | | | | | | | | 2685 |
| 1 | –, xylem[d] | Lumin. | 25.7 | 41.2 | 177.9 | | | | | | | | 2685 |
| *Portulaca grandiflora* Hook. (Rose Moss) | | | | | | | | | | | | | |
| 1 | Callus[u] | IEC | 35.46 | | | 12.53 | | 32.85 | | 4.5 | | | 2686 |
| *Prunus padus* L. (Bird Cherry) | | | | | | | | | | | | | |
| 1 | Phloem exudate[b] | Enzym. | | | 440 | | | | | | | | 2444 |
| *Prunus persica* (L.) Batsch. (Peach) | | | | | | | | | | | | | |
| 1 | Fruit flesh[v] | Lumin. | | 143.7 | 26.0 | | | | | | | | 2687 |
| 2 | Leaf bud[o] | Lumin. | | | 4-20 | | (Other NTP 7-22) | | | | | | 2688 |

*nmol/g fwb unless stated otherwise. [a]Taken from the abstract. [b]μmol/L. [c]μg/plant part. [d]Dry weight basis. [e]nmol/$10^7$ cells. [f]ppm. [g]nmol/plant part. [h]nmol/mg insoluble polysaccharide. [i]μg/g. [j]μg/mL. [k]nmol/$10^6$ protoplasts. [l]μmol/$m^2$. [m]μmol/g. [n]μmol/$10^7$ cells. [o]nmol/mg protein. [p]nmol/mg chlorophyll. [q]Percentage of total free nucleotides. [r]m*M*. [s]mg/g. [t]Percentage P dwb. [u]Total extinction/callus (plant part). [v]counts per minute × $10^3$.

*Continued*

**Table 5-2** Ribonucleotides in Plants*—cont'd

| No. | Plant part | Method | AMP | ADP | ATP | GMP | GDP | GTP | CMP | CDP | CTP | UMP | UDP | UTP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Prunus persica* ssp. *nectarina* (Nectarine) | | | | | | | | | | | | | | | |
| 1 | Fruit flesh[v] | Lumin. | | | 75.5 | | | | | | | | | | 2687 |
| *Prunus sargentii* Rehd. (Sargent Cherry) | | | | | | | | | | | | | | | |
| 1 | Bark[d] | Lumin. | | | 86 | | | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 32 | | | | | | | | | | 2487 |
| *Pseudotsuga menziesii* (Mirb.) Franco (Douglas Fir) | | | | | | | | | | | | | | | |
| 1 | Pollen | Lumin. | | 40-590 | | | | | | | | | | | 2442 |
| *Pteridium aquilinum* (L.) Kuhn (Bracken Fern) | | | | | | | | | | | | | | | |
| 1 | Rhizome[d] | IEC | | | 1.5 | 0.4 | | | | | | 2.8 | | | 2689 |
| *Pyrus communis* L. (Pear) | | | | | | | | | | | | | | | |
| 1 | Fruit pulp[i] | Enzym. | | | 18.9 | | | | | | | | | | 2690 |
| 1 | Bark[d] | Lumin. | | | 89 | | | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 69 | | | | | | | | | | 2487 |
| *Quercus borealis* Michx. f. (Red Oak) | | | | | | | | | | | | | | | |
| 1 | Phloem exudate[b] | Enzym. | | | | 0 | | | | | | | | | 2444 |
| *Quercus mongolica* ssp. *grosseserrata* Rehd. and Wils. | | | | | | | | | | | | | | | |
| 1 | Bark[d] | Lumin. | | | 95 | | | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 57 | | | | | | | | | | 2487 |
| *Quercus petraea* L. ex Liebl. (Durmast Oak) | | | | | | | | | | | | | | | |
| 1 | Phloem exudate[b] | Enzym. | | | 68 | | | | | | | | | | 2444 |
| *Quercus phellos* L. (Willow Oak) | | | | | | | | | | | | | | | |
| 1 | Phloem exudate[b] | Enzym. | | | 68 | | | | | | | | | | 2444 |
| *Quercus robur* L. (English Oak) | | | | | | | | | | | | | | | |
| 1 | Leaf bud[d] | Lumin. | 4 | 3 | 1 | | | | | | | | | | 2446 |
| *Raphanus acanthiformis* Backer (Japanese Radish) | | | | | | | | | | | | | | | |
| 1 | Fruit | IEC | 38 | | | | | | Trace | | | 44 | | | 2456 |
| *Raphanus sativus* L. (Radish) | | | | | | | | | | | | | | | |
| 1 | Seed[a] | Fluorometric | | | + | | | | | | | | | | 2491 |
| 1 | Seed[g] | Lumin. | 2.2 | 0.9 | <0.1 | | | | | | | | | | 2691 |
| 1 | Seed[d] | Lumin. | 578.9 (incl. ADP and ATP) | | | | | | | | | | | | 2495 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Seedling | Lumin. | 29 | 46 | 211 | | | | | | | | 2692 |
| 1 | Root | HPLC | 4 | | | n.d. | | 40 | | 35 | | | 2468 |
| *Ribes sinanense* F. Maekawa | | | | | | | | | | | | | |
| 1 | Bark[d] | Lumin. | | | 206 | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 44 | | | | | | | | 2487 |
| *Ricinus communis* L. (Castor Bean) | | | | | | | | | | | | | |
| 1 | Phloem exudate[b] | TLC/TLC | | + | 400-600 | | | | | | | | 2693 |
| 1 | Phloem exudate[b] | | | | 730 | | | | | | | 140 | 2694 |
| 1 | Phloem exudate[b] | Enzym. | 20 | 80 | 1300 | | | | | | | | 304 |
| *Robinia pseudoacacia* L. (Black Locust) | | | | | | | | | | | | | |
| 1 | Phloem exudate [b] | Enzym. | 6.8 | 7.4 | 50 | | | | | | | | 2444 |
| 1 | Phloem exudate[b] | TLC/TLC | | | + | | 0 | | | | | 0 | 2444 |
| *Rosa damascena* Mill. (Damask Rose) | | | | | | | | | | | | | |
| 1 | Cell susp. culture (*in vivo*) | $^{31}$P NMR | | | | NDP, NTP | | | | | | | 2695 |
| *Saccharum officinarum* L. (Sugar Cane) | | | | | | | | | | | | | |
| 1 | Leaf[q] | PC/PC | 19 | 29 | 7 | – | 12 | | | 21 | – | | 306 |
| 1 | Root[q] | PC/PC | 11 | 21 | 15 | 5 | 9 | | | 17 | 12 | | 306 |
| 1 | Meristem | PC/PC | + | | | | | + | | + | | | 2696 |
| *Salix alba* L. (White Willow) | | | | | | | | | | | | | |
| 1 | Phloem exudate[b] | Enzym. | | | 360 | | | | | | | | 2444 |
| *Salix babylonica* L. (Weeping Willow) | | | | | | | | | | | | | |
| 1 | Bark[d] | Lumin. | | | 27 | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 29 | | | | | | | | 2487 |
| *Salix daphnoides* Vill. | | | | | | | | | | | | | |
| 1 | Phloem exudate[b] | Enzym. | | | 250 | | | | | | | | 2444 |
| *Salix matsudana* Koidz. ssp. *tortuosa* Vilm. (Dragon-Claw Willow) | | | | | | | | | | | | | |
| 1 | Bark[d] | Lumin. | | | 118 | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 51 | | | | | | | | |
| *Salix triandra* L. (Almond Willow) | | | | | | | | | | | | | |
| 1 | Phloem exudate | TLC/TLC | | + | + | | | | + | | | | 309 |
| *Salix viminalis* L. (Basket Willow) | | | | | | | | | | | | | |
| 1 | Sieve-tube sap[i] | Lumin. | | | 850 | | | | | | | | 2697 |

*nmol/g fwb unless stated otherwise. [a]Taken from the abstract. [b]µmol/L. [c]µg/plant part. [d]Dry weight basis. [e]nmol/$10^7$ cells. [f]ppm. [g]nmol/plant part. [h]nmol/mg insoluble polysaccharide. [i]µg/g. [j]µg/mL. [k]nmol/$10^6$ protoplasts. [l]µmol/$m^2$. [m]µmol/g. [n]µmol/$10^7$ cells. [o]nmol/mg protein. [p]nmol/mg chlorophyll. [q]Percentage of total free nucleotides. [r]m*M*. [s]mg/g. [t]Percentage P dwb. [u]Total extinction/callus (plant part). [v]counts per minute × $10^3$.

*Continued*

**Table 5-2** Ribonucleotides in Plants*—cont'd

| No. | Plant part | Method | AMP | ADP | ATP | GMP | GDP | GTP | CMP | CDP | CTP | UMP | UDP | UTP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Sambucus sieboldiana* ssp. *miquelii* Hara | | | | | | | | | | | | | | | |
| 1 | Bark[d] | Lumin. | | | 478 | | | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 117 | | | | | | | | | | 2487 |
| *Sauromatum guttatum* Schott (Voodoo Lily) | | | | | | | | | | | | | | | |
| 1 | Appendix | Lumin. | | 848 | 909 | | | | | | | | | | 2698 |
| *Secale cereale* L. (Rye) | | | | | | | | | | | | | | | |
| 1 | Seed embryo[g] | Lumin. | 0.0 | 0.12 | 0.69 | | | | | | | | | | 2699 |
| 1 | Leaf | HPLC | 37.1 | 60.2 | 50.1 | | | | | | | | | | 2585 |
| *Sequoiadendron giganteum* (Lindl.) Buchholz (Giant Sequoia) | | | | | | | | | | | | | | | |
| 1 | Apex[i] | Lumin. | | | 2.74 | | 1.76 | 0.71 | | | | | | | 2700 |
| 1 | Shoot tip | Lumin. | | | 1200 | | (Other NTP 600) | | | | | | | | 2701 |
| *Sinapis alba* L. (White Mustard) | | | | | | | | | | | | | | | |
| 1 | Seedling[g] | Enzym. | 2.01 | 2.9 | 12.2 | | | | | | | | | | 2702 |
| 1 | Apical bud[g] | Lumin. | 0.118 | 0.008 | 0.010 | | | | | | | | | | 2703 |
| *Solanum melongena* L. (Eggplant) | | | | | | | | | | | | | | | |
| 1 | Seed[g] | Lumin. | | | 0.12 | | | | | | | | | | 2454 |
| *Solanum tuberosum* L. (Potato) | | | | | | | | | | | | | | | |
| 1 | Shoot[d] | Enzym. | | 35,600 | 69,200 | | | | | | | | | | 1099 |
| 1 | Tuber[d] | PC | | | | | | | 80 | | | + | | | 2678 |
| 1 | Tuber | PC/PC | + | + | 10 | | + | + | | | | + | + | + | 9 |
| 1 | Tuber | PC/PE | + | + | 10 | | + | + | | | | + | + | + | 9 |
| 4 | Cooked tuber[i] | TLC/TLC | 17.9-30.0 | | | 12.9-21.1 | | | | | | 16.0-21.4 | | | 2704 |
| 1 | Tuber[q] | IEC | 3.0 | 5.7 | 17.2 | | | | | | | 6.0 | | | 316 |
| 1 | Tuber | CC (cellulose) | 5.5 | 26.2 | 22.8 | 0 | | | | | | 0 | | | 2705 |
| 1 | Tuber | HPLC | 78 | | | n.d. | | | 7 | | | 15 | | | 2468 |
| 1 | Tuber[t] | HPLC | | | n.d. | | | | | | | | | | 696 |
| 5 | Tuber, incubated at 52 °C[i] | HPLC | 0-400 | 210-2200 | 0-1900 | 0-1900 | 150-2000 | 230-2200 | 190-2400 | 0-1800 | 0-920 | 0-220 | 0-500 | 0-2200 | 2706 |
| 1 | Tuber[d] | Enzym. | | 400 | 800 | | | | | | | | | | 1099 |
| 1 | Tuber | Enzym. | 5.3 | 6.4 | 21.6 | | | | | | | | | | 287 |
| 1 | Tuber | Lumin. | | | 3 | | | | | | | | | | 2707 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Tuber | Lumin. | and variation in ADP and ATP content along the stolon-apex axis | | | | | | | | | 533 |
| 1 | –, mitochondria (extract)[o] | $^{31}$P NMR | 0.05 | 0.19 | 0.4 | | | | | | | 2708 |
| 1 | –, starch[m] | IEC | 10.0 | 22.8 | 2.2 | 1.0 | | | 1.3 | | | 2709 |
| *Sonneratia alba* J. Smith | | | | | | | | | | | | |
| 1 | Callus culture | HPLC | 9.8 | 6.4 | 29.7 | 0.7 | 0.4 | 3.1 | | | | 2710 |
| *Sorbus commixta* Hedl. (Mountain Ash) | | | | | | | | | | | | |
| 1 | Bark[d] | Lumin. | | | 71 | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 39 | | | | | | | 2487 |
| *Sorghum bicolor* (L.) Moench (Sorghum) | | | | | | | | | | | | |
| 1 | Seed[d] | Lumin. | 93.3 (incl. ADP and ATP) | | | | | | | | | 2495 |
| 1 | Root tip (*in vivo*) | $^{31}$P NMR | | | | | NDP, NTP | | | | | 44 |
| *Sorghum bicolor* × *Sorghum sudanense* | | | | | | | | | | | | |
| 1 | Seed[g] | Lumin. | 0.67 | | | | | | | | | 2454 |
| *Spartina alterniflora* Loisel. (Smooth Cordgrass) | | | | | | | | | | | | |
| 1 | Leaf[d] | Lumin. | 132 | 802 | 980 | | | | | | | 2711 |
| 1 | –, sheath[d] | Lumin. | 93 | 498 | 1172 | | | | | | | 2711 |
| 1 | Root[d] | Lumin. | 408 | 435 | 1913 | | | | | | | 2711 |
| 1 | Rhizome[d] | Lumin. | 219 | 487 | 1126 | | | | | | | 2711 |
| *Sparlina Cynosuroides* (L.) Roth | | | | | | | | | | | | |
| 1 | Leaf[d] | Lumin. | 131 | 249 | 522 | | | | | | | 2542 |
| *Spartina patens* (Ait.) Muhl. (Saltmeadow Cordgrass) | | | | | | | | | | | | |
| 1 | Leaf[d] | Lumin. | 120 | 347 | 687 | | | | | | | 2711 |
| *Spinacia oleracea* L. (Spinach) | | | | | | | | | | | | |
| 1 | Seed[g] | Lumin. | | | 0.07 | | | | | | | 2454 |
| 1 | Leaf | PC/PC | | | 0 | | | | | | | 2545 |
| 1 | Leaf (extract) | $^{31}$P NMR | + | + | + | | | | + | + | + | 50 |
| 1 | Leaf (*in vivo*) | $^{31}$P NMR | | | | | NDP, NTP | | | | | 50 |
| 1 | Leaf[p] | Enzym. | 8 | 27 | 60 | | | | 4 | 7 | 13 | 322 |
| | | | and subcellular distribution in chloroplast, mitochondria, cytosol and vacuole | | | | | | | | | 2712 |
| 1 | Leaf | Lumin. | 29 | 63 | 133 | | | | | | | 2713 |

*nmol/g fwb unless stated otherwise. [a]Taken from the abstract. [b]µmol/L. [c]µg/plant part. [d]Dry weight basis. [e]nmol/$10^7$ cells. [f]ppm. [g]nmol/plant part. [h]nmol/mg insoluble polysaccharide. [i]µg/g. [j]µg/mL. [k]nmol/$10^6$ protoplasts. [l]µmol/$m^2$. [m]µmol/g. [n]µmol/$10^7$ cells. [o]nmol/mg protein. [p]nmol/mg chlorophyll. [q]Percentage of total free nucleotides. [r]m*M*. [s]mg/g. [t]Percentage P dwb. [u]Total extinction/callus (plant part). [v]counts per minute × $10^3$.

*Continued*

**Table 5-2** Ribonucleotides in Plants*—cont'd

| No. | Plant part | Method | AMP | ADP | ATP | GMP | GDP | GTP | CMP | CDP | CTP | UMP | UDP | UTP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, protoplast[p] | Lumin. | 9.2 | 18.3 | 26.4 | | | | | | | | | | 326 |
| 1 | –, chloroplast[p] | Lumin. | 13.9 | 10.0 | 14.7 | | | | | | | | | | 326 |
| 1 | –, extrachloroplast[p] | Lumin. | 4.1 | 8.5 | 15.3 | | | | | | | | | | 326 |
| 1 | –, chloroplast[p] | IEC | | 7.80 | 2.63 | | | | | | | | | | 20 |
| 1 | –, chloroplast[p] | Lumin. | | 6.29 | 4.79 | | | | | | | | | | 20 |
| 1 | –, chloroplast[d] | Enzym. | 840 | 1360 | 1260 | | | | | | | | | | 2481 |
| 1 | –, chloroplast | $^{31}$P NMR | + | + | + | | | | | | | + | | | 50 |
| *Thalassia testudinum* Koenig and Sims (Turtle Grass) | | | | | | | | | | | | | | | |
| 1 | Leaf[d,i] | Lumin. | | | 524 | | | | | | | | | | 2714 |
| *Tilia platyphyllos* Scop. (Large-leaved Linden) | | | | | | | | | | | | | | | |
| 1 | Phloem exudate[b] | Enzym. | 46.6 | 34.2 | 140 | | | | | | | | | | 2444 |
| 1 | Phloem exudate[b] | TLC/TLC | | | + | | | 0 | | | | | | 0 | 2444 |
| *Tortula ruralis* (Hedw.) Gaertn., Meyer and Scherb. | | | | | | | | | | | | | | | |
| 1 | Whole moss, hydrated | Lumin. | | | 2400 | | | | | | | | | | 2590 |
| *Trifolium incarnatum* L. (Crimson Clover) | | | | | | | | | | | | | | | |
| 1 | Seed[d,g] | Lumin. | 0 | 0.12 | 0 | | | | | | | | | | 2715 |
| *Trigonella foenum-graecum* L. (Fenugreek) | | | | | | | | | | | | | | | |
| 1 | Seed[d] | IEC | 200 | 96.0 | 43.2 | | | | | | | 30 | | | 2716 |
| × *Triticosecale* Wittm. (Triticale) | | | | | | | | | | | | | | | |
| 4 | Seed[g] | Lumin. | | | 0.4-0.8 | | | | | | | | | | 2717 |
| *Triticum aestivum* L. (Wheat) | | | | | | | | | | | | | | | |
| 75 | Seed[d] | Lumin. | | | 1.7-7.1 | | | | | | | | | | 2718 |
| 1 | Seed[d] | Lumin. | 120.0 (incl. ADP and ATP) | | | | | | | | | | | | 2495 |
| 1 | Seed[i] | PC/PC | 1.7 | 7.0 | 2.0 | | | | | | | | | | 2675 |
| 1 | Seed[a] | Fluorometric | | | + | | | | | | | | | | 2491 |
| 1 | Seed[d] | Enzym. | | | 210 | | | | | | | | | | 2719 |
| 1 | Seed caryopsis[g] | Enzym. | 0.58 | 0.94 | 0.34 | | | | | | | | | | 2720 |
| 1 | Leaf[i] | PC/PC | 108.2 | 116.2 | 112.7 | | | | | | | | | | 2675 |
| 1 | Root[i] | PC/PC | 66.2 | – | 80.1 | | | | | | | | | | 2675 |
| 1 | Grain | IEC | 0.67 | 8.8 | 9.5 | 1.1 | | | 12.8 | | | 21.3 | 19.3 | 1.3 | 2721 |
| 1 | Grain, high-yielding[d] | Enzym. | 101.0 | 228.3 | 120.4 | | | | | | | | | | 2722 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Grain, low-yielding[d] | Enzym. | 130.2 | 190.0 | 121.7 | | | | | | | | | | 2722 |
| 1 | Grain | PC/PE | 38 | 77 | 151 | | | | | | | 35 | 135 | 93 | 2723 |
| 1 | –, endosperm | PC/PE | 62 | 119 | 120 | | | | | | | 53 | 186 | 125 | 2723 |
| 1 | –, testa, and pericarp | PC/PE | 24 | 69 | 99 | | | | | | | 32 | 130 | 109 | 2723 |
| 1 | –, aleurone tissue[d] | PC/PC | | 20 | 218 | | | 34 | | | 34 | | 72 | | 2724 |
| 1 | Kernel | IEC | 9.70 | 39.14 | 68.36 | 10.86 | 3.74 | 1.86 | 2.56 | 7.90 | 2.64 | 26.84 | 27.32 | 34.32 | 2633 |
| 1 | Embryo[g] | HPLC | 320 | 98 | 15 | | 78 | 6 | | | n.d. | | 5 | n.d. | 2725 |
| 1 | Embryo[b] | Enzym. | | | | | | | | | | 12.2 | 8.9 | 11.1 | 2726 |
| 1 | Leaf[q] | PE/PC | | 19 | 42 | | | | | | | | 38 | | 331 |
| 1 | Leaf[d,i] | IEC | 26 | | | 17 | | | 13 | | | 20 | | | 2727 |
| 1 | Leaf | HPLC | 22.4 | 35.4 | 39.7 | | | | | | | | | | 2585 |
| 1 | Leaf[l] | Enzym. | | 13 | 46 | | | | | | | | | | 2728 |
| 1 | Leaf | Lumin. | 7 | 20 | 53 | | | | | | | | | | 2729 |
| 1 | –, chloroplast[i] | Lumin. | 6.8 | 13.2 | 27.9 | | | | | | | | | | 2730 |
| 1 | –, mitochondria[i] | Lumin. | −0.2 | 6.1 | 3.2 | | | | | | | | | | 2730 |
| 1 | –, cytosol[i] | Lumin. | 4.7 | 5.2 | 39.1 | | | | | | | | | | 2730 |
| 1 | Mature leaf | Lumin. | 29 | 54 | 59 | | | | | | | | | | 2731 |
| 1 | Leaf and culm | IEC | 2.4 | 2.3 | | | | | | | | | | | 2721 |
| 1 | Aerial parts | IEC | 35 | 49 | 72 | 0 | 14 | 15 | 0 | 0 | 14 | 44 | 52 | 35 | 2432 |
| 1 | Shoot | Lumin. | | | 200 | | | | | | | | | | 2638 |
| 1 | Shoot (*in vivo*) | $^{31}$P NMR | | | | | NTP | | | | | | | | 2638 |
| 1 | Etiolated shoot | IEC | 3800 | 3450 | 950 | 350 | 325 | 200 | 3650 | 325 | 150 | 275 | 1450 | 125 | 2732 |
| 2 | Crown[o] (1) | Lumin. | 0.23 | 2.08 | 3.67 | | | | | | | | | | 2582 |
| | Crown[o] (2) | | 0.12 | 2.01 | 2.68 | | | | | | | | | | 2582 |
| 4 | Crown[d] | Lumin. | | | 550-820 | | | | | | | | | | 2733 |
| 1 | Sprout[g] | Enzym. | 1.0 | 1.48 | 2.74 | | | | | | | | | | 2720 |
| 1 | Embryo | [$^{32}$P]-PEP | | | 8 | | | 46 | | | | | | | 2734 |
| 1 | Embryo | RNA | | | | | | | | | <1 | | | <1 | 2734 |
| 1 | Seedling | PC/PC | + | + | + | + | | | + | | | + | + | + | 2735 |
| 1 | –, coleoptile | PC/PC | + | | | | | | | | | + | | | 2735 |
| 1 | –, root | PC/PC | + | | | | | | | | | + | | | 2735 |

*nmol/g fwb unless stated otherwise. [a]Taken from the abstract. [b]μmol/L. [c]μg/plant part. [d]Dry weight basis. [e]nmol/$10^7$ cells. [f]ppm. [g]nmol/plant part. [h]nmol/mg insoluble polysaccharide. [i]μg/g. [j]μg/mL. [k]nmol/$10^6$ protoplasts. [l]μmol/$m^2$. [m]μmol/g. [n]μmol/$10^7$ cells. [o]nmol/mg protein. [p]nmol/mg chlorophyll. [q]Percentage of total free nucleotides. [r]m*M*. [s]mg/g. [t]Percentage P dwb. [u]Total extinction/callus (plant part). [v]counts per minute × $10^3$.

*Continued*

**Table 5-2** Ribonucleotides in Plants*—cont'd

| No. | Plant part | Method | AMP | ADP | ATP | GMP | GDP | GTP | CMP | CDP | CTP | UMP | UDP | UTP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | –, root | IEC | + | + | + | | | | | | | | | | 2640 |
| 1 | Root and stem | IEC | ++ | + | | + | | | | | | + | | | 2475 |
| *Triticum compactum* Host (Club Wheat) | | | | | | | | | | | | | | | |
| 1 | Leaf | IEC | 42 | 50 | 26 | | | | | | | 33 | 17 | 38 | 2736 |
| *Triticum durum* Desf. (Durum Wheat) | | | | | | | | | | | | | | | |
| 1 | Seed[a] | PC/PE | | | | | | | | | | + | | | 2512 |
| 2 | Embryo | HPLC | 930-943 | 129-164 | | | | | | | | | | | 2737 |
| *Tsuga heterophylla* (Raf.) Sarg. (Western Hemlock) | | | | | | | | | | | | | | | |
| 1 | Pollen | Lumin. | | | 160-550 | | | | | | | | | | 2442 |
| *Ulmus davidiana* Planch. ssp. *japonica* Nakai (Japanese Elm) | | | | | | | | | | | | | | | |
| 1 | Bark[d] | Lumin. | | | 29 | | | | | | | | | | 2487 |
| 1 | Xylem[d] | Lumin. | | | 29 | | | | | | | | | | 2487 |
| *Ulmus glabra* Huds. (Wych Elm) | | | | | | | | | | | | | | | |
| 1 | Phloem exudate[b] | Enzym. | | | 310 | | | | | | | | | | 2444 |
| *Vicia faba* L. (Faba Bean) | | | | | | | | | | | | | | | |
| 1 | Whole plant | IEC | 3.3 | 1.3 | 4.8 | 1.3 | | 1.7 | 10.0 | | | 2.0 | | 6.5 | 2738 |
| 1 | Seed | IEC | 1.9 | 1.4 | 1.5 | 1.3 | | 0.9 | 13.3 | | | 2.1 | | 0.8 | 2738 |
| 1 | Pod | IEC | 0.7 | 0.5 | 0.5 | 0.5 | | 1.2 | 0.5 | | | 0.5 | | 1.3 | 2738 |
| 1 | Guard cell protoplast[m] | Lumin. | 306 | 168 | 660 | | | | | | | | | | 2739 |
| 1 | Chloroplast[m] | Lumin. | 63 | 9 | 18 | | | | | | | | | | 2739 |
| 1 | Mitochondria[m] | Lumin. | 93 | 54 | 201 | | | | | | | | | | 2739 |
| *Vicia sativa* L. (Spring Vetch) | | | | | | | | | | | | | | | |
| 1 | Seed[g] | Lumin. | | | 6.44 | | | | | | | | | | 2454 |
| *Vigna angularis* (Willd.) Ohwi and Ohashi (Adzuki Bean) | | | | | | | | | | | | | | | |
| 1 | Root tip (nmol/mm) | Lumin. | | | 0.028 | and variation in ATP content of 1 mm segments from the tip | | | | | | | | | 2740 |
| *Vigna mungo* (L.) Hepper (Black Gram) | | | | | | | | | | | | | | | |
| 1 | Root nodule | Enzym. | | | 289 | | | | | | | | | | 2741 |
| 1 | Root tip (*in vivo*)[r] | $^{31}$P NMR | | 0..11 | 0.41 | | | | | | | | | | 542,543 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Pod | IEC | 0.7 | 0.5 | 0.5 | 0.5 | | 1.2 | 0.5 | | | 0.5 | | 1.3 | 2738 |
| 1 | Guard cell protoplast[m] | Lumin. | 306 | 168 | 660 | | | | | | | | | | 2739 |
| 1 | Chloroplast[m] | Lumin. | 63 | 9 | 18 | | | | | | | | | | 2739 |
| 1 | Mitochondria[m] | Lumin. | 93 | 54 | 201 | | | | | | | | | | 2739 |
| *Vigna radiata* (L.) Wilcz. (Mung Bean) | | | | | | | | | | | | | | | |
| 1 | Seed[l] | Lumin. | | | 63.0 | | | | | | | | | | 2555 |
| 1 | Whole sprout | IEC | + | + | + | + | + | + | + | + | + | + | | + | 2742 |
| 1 | Sprout | HPLC | 16 | | | 4 | | | n.d. | | | 30 | | | 2468 |
| 1 | Cotyledon[d] | Lumin. | 300 | 285 | 240 | | | | | | | | | | 2524 |
| 1 | Hypocotyl | Lumin. | 12 | 54 | 92 | | | | | | | | | | 2743 |
| 1 | 3-day hypocotyl | IEC | 144 | 28 | 527 | | | | 28 | | | 21 | | 71 | 2744 |
| 1 | 5-day seedling[d] | IEC | 570 | + | | 210 | | | | | | 610 | 400 | | 2433 |
| 1 | Seedling | HPLC | 2 | 62 | 176 | 16 | 9 | 33 | n.d. | n.d. | n.d. | 26 | 25 | 102 | 2441 |
| 1 | Root tip | $^{31}$P NMR | + | + | + | | | | | | | | | | 543 |
| *Viola tricolor* L. (Field Pansy) | | | | | | | | | | | | | | | |
| 1 | Leaf | PC/PC | | | 0 | | | | | | | | | | 2545 |
| *Vitis vinifera* L. (Wine Grape) | | | | | | | | | | | | | | | |
| 1 | Leaf[d,m] | IEC | 5.4 | 5.4 | 5.1 | 23 | 4.9 | 3.4 | 2.0 | 1.8 | | 5.6 | 2.8 | 6.0 | 2745 |
| 1 | Shoot, frost resistant[d,i] | Enzym. | 1.84 | 4.00 | 7.50 | | | | | | | | | | 2746 |
| 1 | Shoot, frost sensitive[d,i] | Enzym. | 1.45 | 3.39 | 5.13 | | | | | | | | | | 2746 |
| 1 | Berry | Enzym. | 0.8 | 9.2 | 29.2 | | | | | | | | | | 333 |
| 2 | Berry | Lumin. | 10-13* | | 35-47 | | | (*Incl. ADP) | | | | | | | 2747 |
| 1 | Berry | Lumin. | Variability in adenine nucleotide content among 50 berries of a single variety (mean ± SD): AMP 3.713 ± 1.079, ADP 2.922 ± 1.207, ATP 20.971 ± 5.836 | | | | | | | | | | | | 2748 |
| *Wolffia arrhiza* (L.) Wimm. (Spotless Water Meal) | | | | | | | | | | | | | | | |
| 1 | Old plant | Enzym. | 14 | 58 | 97 | | | | | | | | | | 2749 |
| *Xanthium pennsylvanicum* Wallr. (Cocklebur) | | | | | | | | | | | | | | | |
| 1 | Seed | Lumin. | 456 | 335 | 501 | | | | | | | | | | 2750 |
| 1 | Root tip | Lumin. | | | 67000 | | | | | | | | | | 2751 |

*nmol/g fwb unless stated otherwise. [a]Taken from the abstract. [b]μmol/L. [c]μg/plant part. [d]Dry weight basis. [e]nmol/$10^7$ cells. [f]ppm. [g]nmol/plant part. [h]nmol/mg insoluble polysaccharide. [i]μg/g. [j]μg/mL. [k]nmol/$10^6$ protoplasts. [l]μmol/$m^2$. [m]μmol/g. [n]μmol/$10^7$ cells. [o]nmol/mg protein. [p]nmol/mg chlorophyll. [q]Percentage of total free nucleotides. [r]m*M*. [s]mg/g. [t]Percentage P dwb. [u]Total extinction/callus (plant part). [v]counts per minute × $10^3$.

*Continued*

**Table 5-2** Ribonucleotides in Plants*—cont'd

| No. | Plant part | Method | AMP | ADP | ATP | GMP | GDP | GTP | CMP | CDP | CTP | UMP | UDP | UTP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Yucca flaccida* Haw. (Weak-Leaf Yucca) | | | | | | | | | | | | | | | |
| 1 | Phloem exudate[j] | TLC/TLC (lumin.) | | + | + (615) | | | | | | + | | | | 309 |
| *Zea mays* L. (Corn) | | | | | | | | | | | | | | | |
| 1 | Seed[d] | Lumin. | 97.3 (incl. ADP and ATP) | | | | | | | | | | | | 2495 |
| 1 | Grain[i] | Lumin. | | | 4200 | | | | | | | | | | 2467 |
| 1 | Kernel, embryo[g] | Lumin. | 3.9 | 1.7 | 0.3 | | | | | | | | | | 2752 |
| 1 | Kernel, embryo[d,i] | Enzym. | 103 | 346 | 291 | | | | | | | | | | 2753 |
| 1 | –, endosperm[d,i] | Enzym. | 85 | 226 | 147 | | | | | | | | | | 2753 |
| 1 | Immature grain | IEC | 240 | | | | | | | | | 532 | | | 2754 |
| 1 | Grain, milky stage | IEC | 10.6 | | | | | | | | | 10 | | | 2755 |
| 1 | Kernel, endosperm[m] | HPLC | 9.10 | 7.32 | 10.89 | | | | | | | 11.48 | 12.04 | 22.98 | 342 |
| 1 | –, starch granule[m] | HPLC | 2.66 | 1.09 | 2.43 | | | | | | | 2.79 | 1.45 | 3.83 | 342 |
| 1 | Leaf | IEC | 25.8 | 64.3 | 146.3 | | 17.2 | 25.0 | | | 5.2 | 1.2 | | 3.2 | 2613 |
| 1 | Leaf[l] | Lumin. | 9.1 | 14.5 | 22.4 | | | | | | | | | | 2574 |
| 1 | Shoot apex[d,g] | Lumin. | | | 1300 | | | | | | | | | | 2756 |
| 1 | Phloem sap[r] | HPLC | 0.26 | 0.82 | 1.52 | 0.00 | 0.17 | 0.32 | 0.00 | 0.00 | 0.00 | 0.06 | 0.14 | 0.42 | 2757 |
| 1 | Pollen[d,i] | Lumin. | | 150 | 2500 | | | | | | | | | | 2758 |
| 1 | Culm[g] | HPLC | 12.7 | 30.8 | 68.7 | | | | | | | | 13.3 | 21.6 | 2759 |
| 1 | Seedling | PC/PC | + | + | + | + | + | + | + | | + | + | + | + | 2735 |
| 1 | –, coleoptile | PC/PC | + | | | | | | | | – | + | | | 2735 |
| 1 | –, root | PC/PC | + | | | | | | | | + | + | | | 2735 |
| 1 | Seedling | IEC | 25.0 | 25.5 | 87.0 | 15.5 | | 17.5 | 4.0 | | 6.5 | 15.5 | 8.0 | 18.5 | 2656 |
| 8 | Seedling, embryo[g] | HPLC | + | + | 16.6-27.9 | | | + | | + | + | | | + | 2760 |
| 1 | Seedling, embryo[g] | Lumin. | | | 11 | | | | | | | | | | 2752 |
| 1 | Seedling, root[i] | IEC | + | 22.5 | 36.4 | + | | 362 | + | | 10.7 | 16.3 | 1.1 | 419 | 2761 |
| 1 | Root | PC/PC | Trace | 107 | 148 | | | | | | + | | | 118 | 12 |
| 1 | Root | TLC/TLC | | + | + | | | + | | | + | | | + | 12 |
| 1 | Root tip[g] | HPLC | 0.22 | 0.81 | 2.13 | | + | + | | + | + | 0.49 | 1.07 | 1.08 | 2759 |
| 1 | Root tip | Lumin. | 28 | 61 | 64 | | | | | | | | | | 2762 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 1 | Root tip (*in vivo*) | $^{31}$P NMR | NDP, NTP | | | 544 |
| *Zostera marina* L. (Seawrack) | | | | | | |
| 1 | Seed pod[d,g] | Lumin. | 108 | 63 | 129 | 2763 |
| 1 | Leaf[d,g] | Lumin. | 47 | 95 | 245 | 2763 |
| 1 | –, sheath[d,g] | Lumin. | 55 | 49 | 72 | 2763 |
| 1 | Root and rhizome[d,g] | Lumin. | 27 | 13 | 34 | 2763 |

*nmol/g fwb unless stated otherwise.
[a]Taken from the abstract.
[b]µmol/L.
[c]µg/plant part.
[d]Dry weight basis.
[e]nmol/$10^7$ cells.
[f]ppm.
[g]nmol/plant part.
[h]nmol/mg insoluble polysaccharide.
[i]µg/g.
[j]µg/mL.
[k]nmol/$10^6$ protoplasts.
[l]µmol/$m^2$.
[m]µmol/g.
[n]µmol/$10^7$ cells.
[o]nmol/mg protein.
[p]nmol/mg chlorophyll.
[q]Percentage of total free nucleotides.
[r]m*M*.
[s]mg/g.
[t]Percentage P dwb.
[u]Total extinction/callus (plant part).
[v]counts per minute × $10^3$.

UMP, UDP, and UTP in PCA extracts of spinach leaf, together with UDPG, UDPGal, and various other phosphorus-containing compounds. According to Lutz *et al.*,[2772] all of the purine and pyrimidine di- and triphosphates in biological tissue extracts can be quantitated by this method alone without using HPLC or any biochemical method.

*(2) Enzyme-Coupled Assay (NAD(P)) Method*

This method, first modified for plant use by Rowan[53] in 1957, enables the individual nucleotides in a plant extract to be quantitated rapidly and accurately without prior separation and, with few exceptions, each assay is specific for the compound being analyzed. The basis of the method is the change in absorbance of NAD (or NADP) at 340 nm, which increases as NAD-(P) is reduced to NAD(P)H and decreases as NAD(P)H is oxidized to NAD(P). Since none of the nucleotides interact directly with NAD(P) or NAD(P)H, each nucleotide must first be converted to a reactive substrate. In theory, any of the reactive substrates shown in Table 1-4 could be used, but the only ones that have achieved broad acceptance are G6P (Table 1-4, reaction 6) for the nucleoside triphosphates and PEP (Table 1-4, reaction 5) for the nucleoside mono- and diphosphates. In the following sections we shall see how these enzyme-coupled reactions are used.

**(A) ADENOSINE PHOSPHATES**

ATP is usually assayed by reaction with glucose in the presence of hexokinase to form G6P, which then reacts with NADP in the presence of G6P dehydrogenase (reaction 6). In a separate analysis, ADP is assayed by reaction with PEP in the presence of pyruvate kinase to form pyruvate, which then reacts with NADH in the presence of lactate dehydrogenase (reaction 5), after which AMP is assayed in the same reaction mixture by addition of myokinase, which converts the AMP to ADP. The amounts of AMP, ADP, and ATP are calculated from the changes in optical density of the NADP or NADH at each stage. The following procedure is typical:

> *Pool sizes of the adenylates, ATP, ADP, and AMP, were measured using assays that coupled adenylate use to NADH or NADPH oxidation/reduction. . . . The ATP assay mixture contained 100 μL of tissue extract and 500 μL of an assay solution containing 100 mM Tris (pH 8.1), 5 mM $MgCl_2$, 1 mM Glc, 260 mM $NADP^+$, and 0.14 unit of Glc-6-P dehydrogenase. The assay was initiated by the addition of 0.42 units of hexokinase in a volume of 1 μL, with 1 mol of NADPH being produced for each mol of ATP consumed in the reaction. The ADP and AMP assay mixtures contained 100 μL of tissue extract and 500 μL of an assay solution 50 mM Hepes (pH 7.6), 5 mM $MgCl_2$, 24 mM NADH, 1.7 mM PEP, 0.4 unit of lactate dehydrogenase, and 16 mM ATP. Determination of ADP was initiated by the addition of 3 units of pyruvate kinase in 2 μL, with 1 mol of NADH being oxidized for each mol of ADP consumed in the reaction. When the ADP assay was completed, AMP was determined by addition of 5 units of myokinase in a 2-μL volume. One mole of NADH oxidized for each 0.5 mol of AMP present in the sample.*
>
> Oresnik, I. J.; Layzell, D. B., "Composition and Distribution of Adenylates in Soybean (*Glycine max* L.) Nodule Tissue", *Plant Physiol.* **1994**, *104*(1), 217–225,[2565] reprinted by permission of the American Society of Plant Biologists, © 1994.

A few investigators[2481,2846] have assayed ATP by reaction with 3-PGA in the presence of phosphoglycerate kinase to form !,3-DPGA which then reacts with NADH in the presence of G3P dehydrogenase (reaction 4, Table 1-4), but this method does not offer any advantage as the ATP still has to be assayed separately from the AMP and ADP. Many investigators have used the test kits provided by Boehringer Mannheim for this purpose.

**(B) URIDINE PHOSPHATES**

UMP, UDP, and UTP can be assayed in a single run using a sequence of enzyme-coupled reactions linked to the reaction of G6P with NAD (reaction 6). UDPG is assayed first with UDPG dehydrogenase [E.C. 1.1.1.22], after which UTP, UDP, and UMP are assayed in turn by the addition of UDPG pyrophosphorylase [E.C. 2.7.7.9], NDP kinase [E.C. 2.7.4.6], and NMP kinase [E.C. 2.7.4.4], respectively.[322] The plant tissue should be extracted with TCA rather than PCA because of the acid-sensitivity of the uridine phosphates.[2712] UDP can also be assayed by an enzyme-coupled reaction linked to the reaction of pyruvate with NADH (reaction 5).[527]

**(C) GUANOSINE AND CYTIDINE PHOSPHATES**

Guanosine and cytidine phosphates should be determinable by this method but there are no examples of these in Table 5-2.

*(3) Firefly Luminescence Method*

This method, first applied to plant extracts by Pradet[2847] in 1967, takes advantage of the unique specificity of American firefly (*Photinus pyralis*) luciferase for ATP. No special precautions are needed to remove phenolics or pigments from a plant extract prior to the assay. Of the 12 most common naturally occurring ribo- and deoxyribonucleoside triphosphates, only one, dATP, generates more than 0.1% of the light produced by ATP.[2848] The intensity of the light, measured in a luminometer, is proportional to the ATP content of the sample over a wide range—from about $10^{-6}$ mol/L to a detection limit of about $5 \times 10^{-14}$ mol/L.[4315] The method can be used for the determination of ATP alone but in most cases the AMP and ADP contents are also needed in order to calculate the "energy charge" of the adenylate system. How this is done is discussed in the following sections.

**(A) ADENOSINE PHOSPHATES**

The enzymes and other reagents used in this method are the same as those used in method 2 but without the NAD(P) or NAD(P)H inasmuch as the end product in each case is ATP. The assays can be carried out sequentially on the same extract, as done by Pradet, or on separate aliquots of the extract as described below.[2670] In the original procedure,[2847] ATP is assayed first, after which PEP and pyruvate kinase are added, converting the ADP to ATP, and when this assay is finished myokinase is added, converting the AMP to ADP, which is in turn converted to ATP by the excess PEP and pyruvate kinase present

in the extract. The amounts of ATP, ADP, and AMP are determined at each stage by the intensity of light released in the luminometer. The following procedure is typical of the method:

> *Four seeds of the designated stage of germination were dissected into gametophyte and embryo or seedling in a moist chamber. . . . Each part was quickly extracted by 10 ml of boiling, glass-distilled water for 10 min at 100 C. The extract was cooled in an ice bath, and 0.8 ml of the . . . extract was incubated at 30 °C for 15 min in each of the following mixtures. A. For ATP determination, 0.1 ml of reaction buffer containing 0.5 M N-2-hydroxyethylpiperazine-N′-2-ethanesulfonic acid (HEPES), pH 7.5, and 0.5 M magnesium acetate and 0.1 ml of glass-distilled water. B. For ADP and ATP determination, 0.1 ml of the reaction buffer and 0.1 ml of a solution containing 20 μg of pyruvate kinase (EC 2.7.1.40) (Sigma, crystalline), and 500 nmoles of trisodium phosphoenolpyruvate (Calbiochem). C. For [total adenosine phosphate], 0.1 ml of the reaction buffer, and 0.1 ml of solution containing 20 μg of pyruvate kinase, 500 nmoles of trisodium phosphoenolpyruvate, and 20 μg of dialyzed (against 1 mM phosphate buffer, pH 7.0) adenylate kinase (EC 2.7.4.3) (Sigma). After incubation, the extracts were either stored at 0 °C overnight or assayed immediately by the luciferin-luciferase method using an Aminco Chem-Glow photometer. . . . Two replications of 0.4 ml each of the above mixtures were added with 100 μl of firefly lantern extract (Sigma FL-E-50; 50 mg of buffered extract in 5 ml of water), containing 50 mM potassium arsenate and 20 mM magnesium sulfate, pH 7.4. The instant peak height of light emission was used for all three mixtures. . . . Based on the peak height of light intensity produced from the three reaction mixtures, ATP concentrations were read directly from a standard curve of freshly prepared ATP solution and the particular batch of enzyme-substrate preparation used for the assay. ATP content of the extract was obtained from reaction mixture A, ADP content was the difference of B and A, and AMP was the difference of C and B. The adenylate energy level of the tissue was calculated to molar concentration by the total ATP and water content in each gametophyte or seedling. The adenylate energy charge is calculated according to Atkinson [*Annu. Rev. Microbiol.* **1969**, 23, 329–337]: Energy charge = ([ATP] + 1/2[ADP])/([ATP] + [ADP] + [AMP]).*
>
> Ching, T. M.; Ching, K. K., "Content of Adenosine Phosphates and Adenylate Energy Charge in Germinating Ponderosa Pine Seeds", *Plant Physiol.* **1972**, *50*(5), 536–540,[2670] reprinted by permission of the American Society of Plant Biologists, © 1972.

Though the light emission is in most cases measured by peak height, it can also be measured by integration of the light emitted over a period of 10 s,[2477] or by liquid scintillation counting,[2718] depending on the capability of the instrument. In some cases, the conversion of ADP to ATP has been done by substituting creatine phosphate for the PEP[2687] or of creatine phosphotransferase [E.C. 2.7.3.2] for the phosphokinase.[2687]

**(B) OTHER NUCLEOSIDE PHOSPHATES**

Nucleoside triphosphates other than ATP, labeled "other NTP" in Table 5-2, can be determined by the bioluminescence method after conversion to ATP by incubation with nucleoside diphosphate kinase [NDPK, E.C. 2.7.4.6] in the presence of excess ATP. The increase in the ATP level corresponds to the NTP level of the extract.[2849] GTP can be determined by incubation of the extract with succinic thiokinase [E.C. 6.2.1.4], which consumes the GTP prior to treatment with NDPK and ATP:

$$[\text{GTP}] = [\text{ATP}]_{\text{endogenous}} + [\text{ATP}]_{\text{NDPK}} - [\text{ATP}]_{\text{thiokinnase}}.^{2700}$$

Similarly, UTP can be determined by incubation of the extract with UDPG pyrophosphorylase [E.C. 2.7.7.9] in the presence of excess G1P, which consumes the UTP prior to treatment with NDPK and ATP:

$$[\text{UTP}] = [\text{ATP}]_{\text{endogenous}} + [\text{ATP}]_{\text{NDPK}} - [\text{ATP}]_{\text{pyrophosphorylase}}.^{2478}$$

*(4) Polymerase (RNA) Method*

This method, which was used to determine the cellular levels of CTP and UTP in germinating wheat embryos,[2734] is based on the ability of the enzyme RNA polymerase [E.C. 2.7.7.6] to catalyze the formation of an acid-insoluble RNA polymer in the presence of a suitable primer. [$H^3$]-ATP was used in the assay and the levels of the two nucleotides were determined by collecting the precipitated RNA and measuring its tritium content by scintillation counting.

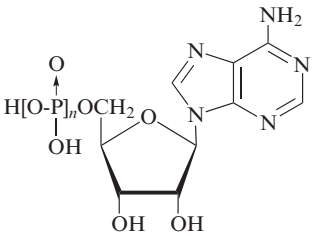
*(5) [$^{32}P$]-Labeled PEP Method*

This method, which was used to determine the cellular levels of ATP and GTP in germinating wheat embryos,[2734] is based on the phosphorylation of ADP or GDP by [$^{32}$P]-labeled PEP in the presence of pyruvate kinase [E.C. 2.7.1.40]. The extent of labeling provides a direct measure of the ATP (or GTP) content; neither enzyme coupling to NAD(P) nor bioluminescence is required for this assay. The endogenous ATP is converted quantitatively to ADP by hexokinase in the presence of excess G1P prior to [$^{32}$P] labeling, and this same reaction is used to remove [$^{32}$P]-labeled ATP when assaying for GTP.[2734]

# RIBONUCLEOTIDES

This group comprises the adenosine derivatives AMP, ADP, and ATP, the guanosine derivatives GMP, GDP, and GTP, the cytidine derivatives CMP, CDP, and CTP, and the uridine derivatives UMP, UDP, and UTP (Y=OH in the formula on p 289).

# Adenosine Phosphates



AMP, $n = 1$
ADP, $n = 2$
ATP, $n = 3$

## Physical Properties

Adenosine 5′-phosphate (AMP), $C_{10}H_{14}N_5O_7P$. *5′-Adenylic Acid*
AMP [R.N. 61-19-8]: Filamentary crystals,[2850] mp 208 °C dec.,[2851] $[\alpha]_D^{20}$ − 26.0°(10% HCl), −47.5° (2% NaOH),[2852] specific volume 0.53 at 24 °C[2853]; conductivity (calc.)[2854]; polarographic reduction[2855]; diamagnetic susceptibility ($\chi_m$) $-171 \times 10^{-6}$ $cm^3$/mol at 25 °C[410]; countercurrent distribution[2856]; hydrophobicity[2857]; fluorescence,[2858] phosphorescence,[2859] bioluminescence.[2860] Ionization constants: p$K_a$ 0.89, 3.70, 6.01 (potentiometric, 25 °C),[2861] 13.06 (thermometric, 25 °C),[354] 3.7, 6.1 (UV, 25 °C),[2862] <1.2, 3.9, 6.7 ($^1$H NMR, 32 °C),[2863] 6.11 ($^{31}$P NMR).[68] Spectra: UV[2862] (fig.),[2864] IR (fig.),[2865] FTIR (fig.),[2866] Raman (fig.)[2867] ORD (fig.),[2868] CD (fig.),[2869] PES,[2870] ESR,[2871] tunneling (fig.),[2872] ultrasound (fig.),[2873] ultrasonic absorption coefficients.[2874] [$^1$H] NMR (fig.),[2875] 2d-[$^1$H] NMR,[2876] [$^{13}$C] NMR (fig.),[2877] [$^{14}$N] NMR,[2878] [$^{15}$N] NMR (fig.),[2879] [$^{17}$O] NMR (fig.),[2880] [$^{31}$P] NMR,[68] 2d-[$^{13}$C,$^{15}$N] NMR (fig.),[2881] 2d-[$^{13}$C,-$^{31}$P] NMR (fig.).[2882] Mass spectra: EI-MS,[2883] FD-MS,[2884] FAB-MS,[2885] SI-MS,[2886] ESI-MS,[2887] EH-MS,[2888] LM-MS,[2889] FAB-MS/MS,[2890] ES-MS/MS.[2814] Chromatography: PC,[9] TLC, [36] HPTLC,[2891] GC (TMS derivative),[2892] GFC,[2893] IEC,[2894] HPLC,[2440] preparative HPLC,[2895] column (activated carbon).[2896] Electrophoresis: PE,[32] TLE,[36] isotachophoresis,[2897] moving boundary (fig.),[2898] CE,[2899] CZE,[2900] MEKC.[2901] Theoretical calculations: LCAO-MO,[116] PCILO,[2902] EHT,[2903] CNDO,[2904] $\Delta G°$,[2905] mol. polarizability and diamagnetic susceptibility.[2906] *AMP·$H_2O$* [R. N. 18422-05-4]: Needles (photo), dec. 195 °C (sealed tube), $[\alpha]_D^{20}$ − 38.0°(10% HCl), −59.5° (2% NaOH), $[\alpha]_D^{50}$ − 40.5°($H_2O$); least water soluble of the four RNA nucleotides[2907]; long, thin monoclinic needles, $d_c$ 1.647, X-ray structure.[2908]
$Na_2C_{10}H_{12}N_5O_7P{\cdot}nH_2O$ [R.N. 146877-92-1]: FTIR (fig.),[2909] Raman,[2910] FAB-MS,[2911] dielectric properties (TSDC, fig.).[2912] *Dodecahydrate* [R.N. 177980-01-7]: Orthorhombic crystals, X-ray structure.[2913]
$MgC_{10}H_{12}N_5O_7P{\cdot}5H_2O$: Cryst. solid, FTIR (fig.).[2866] Hexahydrate, Raman (fig.).[2914]
$CaC_{10}H_{12}N_5O_7P{\cdot}6H_2O$: Cryst. solid, FTIR (fig.).[2866]
$BaC_{10}H_{12}N_5O_7P{\cdot}7H_2O$ [R.N. 61240-11-7]: Clear, platelike monoclinic crystals, $d_m$ 1.91, $d_c$ 1.886, X-ray.[2915] IR,[2916] FTIR (fig.),[2866] Raman (fig.).[2914]
$(C_{23}H_{26}N_2O_4)_2C_{10}H_{14}N_5O_7P$ (brucine salt): mp 180-182 °C.[2851]

$(C_{13}H_9N)_2C_{10}H_{14}N_5O_7P{\cdot}H_2O$ (acridine salt): Egg-yellow, dense prismatic needles, mp 208 °C,[2917] $[\alpha]_D^{20}$ − 46.4°($H_2O$).[1442]
Also given: FTIR (fig.) for the Li, Cs, and $NH_4$ salts of AMP and data for the K and Rb salts.[2909]

Adenosine 5′-Diphosphate (ADP), $C_{10}H_{15}N_5O_{10}P_2$. *Adenosine 5′-(Trihydrogen Diphosphate)*.

ADP [R.N. 58-64-0]: $[\alpha]_D^{25}$ − 25.7°($H_2O$),[2918] countercurrent distribution,[2856] liquid-liquid extraction,[2919] fluorescence,[2858] phosphorescence,[2859] bioluminescence,[2860] polarographic reduction,[2855] ODMR,[2920] diamagnetic susceptibility ($\chi_m$) $-196\times10^{-6}$ $cm^3$/mol at 25 °C[410]; ionization constants: p$K_a$ 3.95, 6.26 (potentiometric, 25 °C),[2921] 3.9, 6.3 (UV, 25 °C).[2862] Spectra: UV (fig.),[2864] IR (fig.),[2922] ORD (fig.),[2923] Raman (fig.),[2924] ultrasound (fig.),[2873] ultrasonic absorption coefficients,[2874] EPR (no signal),[2925] [$^1$H] NMR,[461] [$^{13}$C] NMR (fig.),[2926] [$^{17}$O] NMR (fig.),[2927] [$^{31}$P] NMR,[68] 2d-[$^1$H] NMR (fig.),[2928] ESI-MS,[2887] SI-MS.[2929] Chromatography: PC,[9] TLC,[36] HPTLC,[2891] GFC,[2930] IEC,[2894] HPLC.[2440] Electrophoresis: PE,[32] TLE,[36] isotachophoresis,[2897] moving boundary (fig.),[2898] MEKC.[2901] CZE,[2900] Theoretical calculations: LCAO-MO,[116] EHT,[2931] CNDO.[2904] *ADP·3H$_2$O* [R.N. 72636-41-0]: Needles (photo),[2932] $d_m$ 1.64, $d_c$ 1.64, X-ray structure[2933]; piezoelectric properties.[2934]
$NaC_{10}H_{14}N_5O_{10}P_2{\cdot}H_2O$ [R.N. 1172-42-5]: White powder, $^1$H, $^{23}$Na, $^{31}$P NMR.[2935]
$Na_2C_{10}H_{13}N_5O_{10}P_2$: Dielectric properties (TSDC, fig.).[2912]
$KC_{10}H_{14}N_5O_{10}P_2{\cdot}2H_2O$ [R.N. 72696-48-1]: Thin orthorhombic needles, $d_c$ 1.771, X-ray structure[2936]; $d_m$ 1.81, $d_c$ 1.82.[2937]
$(C_{13}H_9)N{\cdot}C_{10}H_{15}N_5O_{10}P_2{\cdot}H_2O$ (acridine salt): Egg-yellow prismatic needles, mp 215 °C dec.,[2917] X-ray powder pattern.[2938]

Adenosine 5′-Triphosphate (ATP), $C_{10}H_{16}N_5O_{13}P_3$. *Adenosine 5′-(Tetrahydrogen Triphosphate)*.

ATP [R.N. 56-65-5]: Fluorescence,[2858] phosphorescence,[2859] bioluminescence,[2860] countercurrent distribution,[2856] liquid-liquid extraction,[2919] polarographic reduction,[2855] diamagnetic susceptibility ($\chi_m$) $-226\times10^{-6}$ $cm^3$/mol at 25 °C[410]; dipole moment (*D*) 230 esu cm.[2939] Ionization constants: p$K_a$ 4.00, 6.48 (potentiometric, 25 °C),[2921] 4.1, 6.5 (UV, 25 °C),[2862] other acidic groups.[2940] Spectra: UV (fig.),[2862] far UV,[2941] IR (fig.),[2942] Raman (fig.),[2924] ORD,[2943] CD,[2944] ultrasound,[2945] ultrasonic absorption coefficients,[2874] [$^1$H] NMR (fig.),[2875] [$^{13}$C] NMR (fig.),[2946] [$^{17}$O] NMR (fig.),[2880] [$^{31}$P] NMR,[68] 2d-[$^1$H] NMR (fig.),[2928] PES,[2870] FAB-MS,[2947] ESI-MS,[2887] SI-MS.[2929] Chromatography: PC,[9] TLC,[36] HPTLC,[2891] GFC,[2893] IEC,[2894] HPLC,[2440] preparative HPLC.[2895] Electrophoresis: PE,[32] TLE,[36] isotachophoresis,[2897] moving boundary (fig.),[2898] CE,[2899] CZE,[2900] MEKC.[2901] Theoretical calculations: LCAO-MO,[116] EHT,[2931] CNDO,[2904] $\Delta G^\circ$.[2905]
$Na_2C_{10}H_{14}N_5O_{13}P_3$ [R.N. 987-65-5]: Extremely stable both in the dry state and in neutral solution.[2948] *Trihydrate* [R.N. 51963-61-2]: Crystalline solid (photo), mp 188 °C dec.[2949]; very thin orthorhombic blades, $d_m$ 1.785, $d_c$ 1.787, X-ray structure[2950]; molar conductance ($\Lambda_M$).[2951] Spectra: IR,[2951] Raman (fig.),[2952] $^1$H, $^{23}$Na, and $^{31}$P NMR,[2935] EPR (fig.),[2925] FAB-MS,[2953] ES-MS.[2954]

$BaC_{10}H_{14}N_5O_{13}P_3$ [R.N. 22887-43-0]: Amorphous solid, unstable in air disproportionating in part into ADP and adenosine 5′-tetraphosphate[2948]; IR, molar conductance ($\Lambda_M$).[2951]
$Ba_2C_{10}H_{12}N_5O_{13}P_3$ [R.N. 22887-44-1]: Amorphous solid, stable when dry but slightly degraded in air[2948]; forms a hexahydrate when left in air 2 weeks[2955]; IR, molar conductance ($\Lambda_M$)[2951]; X-ray diffraction pattern.[2956]
$(C_{13}H_9N)_3C_{10}H_{16}N_5O_{13}P_3{\cdot}H_2O$ (acridine salt): Air-stable, hygroscopic egg-yellow needles, mp 208-209 °C dec.[2957]
Other salts: ATP, unlike other phosphate esters, does not form crystalline salts with morphine, brucine, or strychnine, nor with heavy metal (Ag, Hg, Cu) or alkaline earth (Ca, Ba) bases.[2917]

## Conformation

In the solid state, according to X-ray analysis, the plane of the ribose ring in AMP is at a dihedral angle of 76° with respect to the plane of the adenine ring, both being slightly puckered. The relative orientation of the ribose and adenine rings is *anti*. In aqueous solution, according to [$^{31}$P]-$^1$H NMR analysis, the AMP molecule is flexible with respect to the ribose residue, undergoing interconversion between the two preferred conformations, $^3$E and $^2$E (or N and S), where $^3$E is 3′-*endo* and $^2$E is 2′-*endo*. The ratio of $^3$E to $^2$E is 27:63 at concentrations below 0.01*M*, over 1:1 at concentrations over 2.0*M*, and all $^3$E in the solid state.[2958] With regard to the exocyclic $CH_2OP(O)(OH)_2$ group, which is flexible in aqueous solution, there are six possible rotamers: three for the C(4′)—C(5′) bond (gg, gt, and tg) and three for the C(5′)—O(5′) bond (g′g′, g′t′, and t′g′). The preferred conformation of AMP in neutral aqueous solution is *anti* gg-g′g′. See Evans and Sarma[2958] for Newman projections and other details.

The conformation of ADP in the solid state, based on X-ray analysis of the free acid[2933] and its potassium salt,[2936,2937] is similar to that of AMP. The orientation is *anti trans* gg in both acid and salt. In neutral aqueous solution, however, the orientation (according to $^1$H NMR analysis) is only 20% *anti*.[2959] The diphosphate chain is extended rather than folded as in ATP. The ribose unit is predominantly $^2$E and the base lends only a small contribution to the *syn* conformation of the molecule.[2960] A theoretical study of ADP by the EHT method indicates that the adenosine part has three preferred conformations whereas the diphosphate part is able to adapt its conformation to the environmental conditions.[2931]

The triphosphate chain in the crystalline disodium salt of ATP is in a folded conformation in each of two crystallographically independent molecules, folded to form part of a left-handed and right-handed helix, respectively.[2950] This geometry seems to be maintained in neutral aqueous solution. One of the preferred conformations, determined by the effect of lanthanide shift reagent on its $^1$H and $^{31}$P NMR spectra, corresponds closely to the crystal form having the right-handed helical phosphate chain.[2961] This conclusion is supported by molecular orbital[2962] and classical potential energy[2963] calculations which indicate that the terminal phosphate group may be even closer to the adenine ring in

the free molecule than in the crystal.[2962] In aqueous solution, the conformation about the glycosyl bond is *syn* but changes to *anti* if the pH is above 12; the thermodynamics of this isomerization were determined by an ultraviolet relaxation method.[2874]

## Synthesis

AMP may be prepared (a) by phosphorylation of 2′,3′-*O*-isopropylideneadenosine with $POCl_3$[2964] or $P_2O_3Cl_4$,[2965] with morpholino[2966] or phenyl[2967] phosphorodichloridate, with *o*-phenylene,[2968] diallyl,[2969] or bis(2,2,2-tribromoethyl)[2970] phosphorochloridate, or with 8-quinolyl,[2971] *p*-nitrophenyl,[2972] or 2-cyanoethyl[2973] dihydrogen phosphate; (b) by phosphorylation of 2′,3′-*O*-benzylideneadenosine with dibenzyl phosphorochloridate[2974] or of 2′,3′-*O*-diacetyladenosine with benzylphosphorous diphenylphosphoric anhydride[2975]; (c) by phosphorylation of unprotected adenosine with $POCl_3$,[2976] $P_2O_3Cl_4$,[2965] di(2-*t*-butylphenyl) phosphorochloridate,[2977] or tris(8-quinolyl) phosphate[2978]; or (d) by fusion of 2,3-di-*O*-benzoyl-5-(diphenylphosphonooxy)-D-ribofura-nosyl bromide with 6-benzamidopurine[2979] or its bis(trimethylsilyl) derivative.[2980]

ADP may be prepared (a) from 5′-*O*-tosyladenosine by reaction with tris(tetra-*n*-butylammonium) pyrophosphate[2981]; (b) from AMP by condensation with phosphoric acid in the presence of dicyclohexylcarbodiimide,[2982] 1,1′-carbonyldiimidazole,[2983] or cyclopentanone oxime *p*-nitrobenzenesulfonate[2984]; (c) from AMP by phosphorylation with benzyl *N*-cyclohexylphos-phoramidate,[2985] dibenzyl phosphorochloridate,[2986] phosphoric triimidazolide,[2987] or 2-cyanoethyl α-pyridyl phosphate[2988]; (d) from an AMP anhydride by reaction with tri-*n*-butylammonium phosphate[2989,2990]; (e) from adenosine 5′-phosphoramidate[2991] or N-substituted phosphoramidate by reaction with anhydrous phosphoric acid[2992–2994]; (f) from other AMP derivatives containing protecting substituents at the 2′-OH and 3′-OH positions,[2995,2996] or (g) from ATP by partial hydrolysis[2997] or methanolysis.[2998]

ATP may be prepared (a) from adenosine by phosphorylation with $POCl_3$ in trimethyl phosphate followed by reaction with tri-*n*-butylammonium phosphate[2999] or bis(tri-*n*-butylammonium) pyrophosphate[3000]; (b) from 5′-*O*-tosyladenosine by reaction with tetrakis(tetra-*n*-butylammonium) triphosphate[2981]; (c) from AMP by condensation with phosphoric acid in the presence of dicyclohexylcarbodiimide,[2981] cyclopentanone oxime *p*-nitrobenzenesulfonate[2984] or 8-(5-chloroquinolyl) *S*-phenylphosphorothioate[3001]; (d) from AMP by phosphorylation with dibenzyl phosphorochloridate,[3002] phosphoric triimidazolide,[2987] or pyrophosphoric tetraimidazolide[3003]; (e) from AMP by enzymatic phosphorylation with acetyl phosphate (preferably the sodium salt[3004]) as the ultimate phosphate donor[3005]; (f) from adenosine 5′-phosphoramidate[3006] or phosphoromorpholidate[3007] by reaction with a bis(trialkylammonium) pyrophosphate; (g) from ADP by phosphorylation with acetyl phosphate in the presence of Fe(III) or [24]-$N_6O_2$ polyamine catalyst,[3008,3009] with tri(*n*-butylammonium) phosphate in the presence of 1,1′-carbonyldiimidazole[2983] or by reaction with benzyl *N*-cyclohexylphosphoramidate[2985]; or (h) from various other AMP or ADP derivatives containing protected OH groups.[2957,2995,3010–3012]

## Hydrolysis

AMP is stable to hydrolysis under alkaline conditions but somewhat less stable under neutral or mildly acid conditions.[205] At intermediate pH (5-9) the hydrolysis follows pseudo-first-order kinetics, giving only the products of P—O bond cleavage, adenosine, and $P_i$. At pH 5, the first-order rate constant increases steadily from 0.000231 $h^{-1}$ (half-life 3000 h) to 0.816 $h^{-1}$ (half-life 0.85 h) as the temperature is raised from 53 °C to 121 °C.[3013] At pH 3 and 100 °C, in the absence of buffer, the products of N—C bond cleavage, adenine and ribose, also appear.[3013,3014] Under much milder conditions (pH 8.6, 37 °C), the hydrolysis of AMP is catalyzed by Ce(III) and other heavy metal ions[3015] and by lanthanide complexes.[3016] Hydrolysis of AMP with 1*N* $H_2SO_4$ liberates only 1% of $P_i$ after 30 min at 100 °C.[3017] Hydrolysis with 4% HCl liberates all of the adenine but no $P_i$.[3018] The probable course of this reaction is discussed below under GMP.

The hydrolysis of ADP to AMP and $P_i$ in aqueous solution at 80-95 °C is first order with respect to ADP and is catalyzed by $H^+$. The activation energy at pH 8.0 is 24.2 kcal/mol.[3019] The hydrolysis is also catalyzed by bivalent metal ions, notably Cu(II),[3020] by Ce(III) and other heavy metal ions,[3021,3022] and by macrocyclic polyamines such as [24]-$N_6O_2$.[3023] Tracer studies with $^{18}O$-enriched water show that bond fission occurs at both sides of the anhydride oxygen resulting in a partially labeled $P_i$, but there is no evidence of oxygen isotope exchange with the solvent.[3024]

The hydrolysis of ATP to ADP and $P_i$ in aqueous solution is first order with respect to ATP and is catalyzed by $H^+$. The rate constant $k$ decreases from about $4 \times 10^{-6}$ $s^{-1}$ at pH 2 to about $10^{-7}$ $s^{-1}$ at pH 9.5 (50 °C, $I = 0.1$).[3025] The hydrolysis is also catalyzed by bivalent metal ions, notably Cu(II),[3020] by Ce(III) and other heavy metal ions,[3021,3022] and by macrocyclic polyamines such as [24]-$N_6O_2$.[3023] The effectiveness of the bivalent metal ions decreases in the order Cu(II) > Cd(II) > Zn(II) Ni(II) > Mn(II) > Mg(II) and differs from one nucleotide to another, whereas the first-order rate constants for the uncomplexed nucleotides (ATP, GTP, CTP, and UTP) are virtually identical.[3026] The hydrolysis of ATP is complicated by the liberation under certain conditions of pyrophosphate[3014,3024] or metaphosphate[3027] and by further degradation of the ribose 5-phosphate to ribose and $P_i$.[3028]

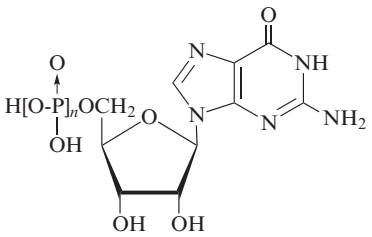
## Phosphorylation

Methods for the phosphorylation of AMP to ADP or ATP and of ADP to ADP are discussed under the section "Synthesis" above. These methods, which result in an extension of the phosphate chain, employ either a phosphorylating agent containing a reactive P—Cl, P—N, or P—O bond or a condensing agent to link a $P_i$ to the terminal phosphate group. In the absence of a catalyst, reaction with AMP with sodium trimetaphosphate, best carried out in aqueous solution at pH 12 over a period of 20-30 days at room temperature, yields a 1:1 mixture of 2′,5′-ADP and 3′,5′-ADP, products of phosphorylation of the remaining free OH groups of the ribose ring.[3029] In the presence of Mg(II) catalyst, the reaction takes a different course giving within 1-2 days under ambient conditions a mixture of adenosine

5′-polyphosphates $P_nA$ where A = adenosine and $n = 4$, 7, and 10.[3030] ADP, under the same conditions, yields a mixture of adenosine polyphosphates $P_nA$ where $n = 5$, 8, and 11.[3030]

Phosphorylation of AMP with $KH_2PO_4$ under prebiotic conditions (formamide, 110 °C) for 12 h yields a mixture of 2′-, 3′-, and 5′-AMP, 2′,3′-cyclic AMP, and several diphosphates, like that obtained with adenosine under the same conditions.[3031]

# Guanosine Phosphates




GMP, $n = 1$
GDP, $n = 2$
GTP, $n = 3$

## Physical Properties

Guanosine 5′-Phosphate (GMP), $C_{10}H_{14}N_5O_8P$. *5′-Guanylic Acid*.

GMP [R.N. 85-32-5]: Fluorescence,[3032] phosphorescence,[3033] chemiluminescence,[3034] polarography,[3035] lactim-lactam tautomerism,[3036] hydrophobicity,[2857] countercurrent distribution.[2856] Dipole moment (*D*) 166 esu cm[2939] (calc. $\mu$ 11.6, $\theta$ 10[3037]), liquid crystals.[3038] Ionization constants: p$K_a$ 0.7, 2.3, 5.92, 9.36 (potentiometric, 25 °C),[2861] 2.4, 6.1, 9.4 (UV, 25 °C),[2862] <2.1, 6.2 ($^1$H NMR, 32 °C),[2863] 6.15 ($^{31}$P NMR, 22 °C).[68] Spectra: UV (fig.),[2864] IR (fig.)[3039] FTIR (fig.),[3040] Raman (fig.),[3041] ORD (fig.),[3042] CD (fig.),[3043] PES (fig.),[2870] ESR,[2871] [$^1$H] NMR (fig.),[3044] [$^{13}$C] NMR (fig.),[3045] [$^{15}$N] NMR,[2879] [$^{31}$P] NMR,[68] 2d-[$^1$H] NMR (fig.),[3046] ultrasound,[3047] EI-MS,[2883] FAB-MS,[3048] SI-MS,[2886] FAB-MS/MS.[2890] Chromatography: PC,[9] TLC,[3049] HPTLC,[2891] IEC,[2894] HPLC,[2440] preparative HPLC,[2895] GC (TMS derivative),[2892] GFC,[2893] column (activated carbon.).[2896] Electrophoresis: PE,[9] TLE,[3050] CZE,[2900] isotachophoresis,[2897] MEKC.[2901] Theoretical calculations: PCILO,[3051] CNDO.[3052] *GMP·2H$_2$O*: Long tapering needles (photo),[2907,3053] mp 180 °C (sealed capillary),[2907] $[\alpha]_D^{20}$ − 13.5°($H_2O$), −48.5° (5% $NH_4OH$),[3053] $[\alpha]_D^{25}$ − 7.5°($H_2O$), +1.5° (10% HCl), −57.0° (2% NaOH).[2907] *GMP·3H$_2$O* [R.N. 26166-34-7]: Orthorhombic needle-shaped crystals, $d_m$ 1.644, $d_c$ 1.650, X-ray structure.[3054,3055] Conformation similar to AMP but unlike IMP.[3054]
$NaC_{10}H_{13}N_5O_8P$: IR (fig.),[3039] FAB-MS/MS.[2890]
$Na_2C_{10}H_{12}N_5O_8P$ [R.N. 5550-12-9]: IR (fig.).[3039] *Tetrahydrate* [R.N. 20813-77-8]: Monoclinic crystals, $d_m$ 1.705, TGA, dielectric relaxation, X-ray structure.[3056] *Heptahydrate* [R.N. 20813-78-9]: Orthorhombic crystals, $d_m$ 1.69, $d_c$ 1.65, X-ray structure,[3057] far IR (fig.),[2769] FTIR (fig.),[2909] Raman (fig.),[3058] [$^{23}$Na] NMR,[3059] FAB-MS,[2911] TGA,[3056] dielectric relaxation.[3056]

$BaC_{10}H_{12}N_5O_8P{\cdot}2H_2O$ [R.N. 3387-75-5]: IR (fig.).[3039] *Hexahydrate* [R.N. 143256-05-7]: Rectangular orthorhombic crystals, $d_c$ 1.970, X-ray structure.[3060]
$(C_{23}H_{26}N_2O_4)_2C_{10}H_{14}N_5O_8P{\cdot}7H_2O$ (brucine salt): mp 233 °C, $[\alpha]_D^{20}$ − 26.0° (35% ethanol).[3061]
Other salts: FTIR (figs.) for the Li, Cs, and $NH_3$ salts of GMP and data for the K and Rb salts.[2909]

Guanosine 5′-Diphosphate (GDP), $C_{10}H_{15}N_5O_{11}P_2$. *Guanosine 5′-(Trihydrogen Diphosphate)*.

GDP [R.N. 146-91-8]: Liquid-liquid extraction,[2919] countercurrent distribution,[2856] bioluminescence,[2860] chemiluminescence.[3034] Ionization constants: p$K_a$ 7.19 (potentiometric, 25 °C),[3062] 2.9, 6.3, 9.6 (UV, 25 °C).[2862] Spectra: UV (fig.),[2864] PES (fig.),[2870] CD (fig.),[3063] [$^1$H] NMR,[3044] [$^{31}$P] NMR.[68] Chromatography: PC,[9] TLC,[36] HPTLC,[2891] IEC,[2894] GFC,[2930] HPLC,[2440] preparative HPLC.[2895] Electrophoresis: PE,[9] TLE,[36] CZE,[2900] isotachophoresis,[2897] MEKC.[2901]
$Na_2C_{10}H_{13}N_5O_{11}P_2$ [R.N. 7415-69-2]: FAB-MS.[2911]

Guanosine 5′-Triphosphate (GTP), $C_{10}H_{16}N_5O_{14}P_3$. *Guanosine 5′-(Tetrahydrogen Triphosphate)*.

GTP [R.N. 86-01-1]: Bioluminescence,[2860] chemiluminescence,[3034] countercurrent distribution,[2856] liquid-liquid extraction,[2919] polarographic reduction,[3035] lactim-lactam tautomerism.[3036] Ionization constants: p$K_a$ 7.65, 9.6 (potentiometric, 25 °C),[3062,3064] 3.3, 6.5, 9.3 (UV, 25 °C).[2862] Spectra: UV (fig.),[2862] PES (fig.),[2870] [$^1$H] NMR,[3044] [$^{31}$P] NMR,[68] FAB-MS.[2911] Chromatography: PC,[9] TLC,[36] HPTLC,[2891] GFC,[2930] IEC,[2894] HPLC,[2440] preparative HPLC.[2895] Electrophoresis: PE,[9] TLE,[36] CZE,[2900] isotachophoresis,[2897] MEKC.[2901]
$Na_3C_{10}H_{13}N_5O_{14}P_3$ [R.N. 36051-31-7]: ES-MS.[2954]

## Conformation

The conformation of GMP in the crystalline disodium[3057] and barium[3060] salts is identical to that of AMP, and likewise shows a preference for the *anti* ($^2E \leftrightarrow {}^3E$) gg-g′g′ conformation in neutral aqueous solution.[3065] Temperature has little effect on this conformation, but if the pH is reduced to 4 or less (the pK at which the base is protonated at $N^7$) the ribose conformation changes from S to N, the exocyclic rotamer distribution changes, but the *anti* conformation remains the same.[3044] In contrast, the tetrabutylammonium salt of GMP dissolves in dimethylformamide forming aggregates in which the GMP has the *syn* conformation.[3046]

The conformation about the glycosidic bond in both GDP and GTP is predominantly *syn* (>90%) in aqueous solution, according to $^1$H NMR. The β-phosphate group is oriented toward the pyrimidine base and close to H(3′).[2959]

## Synthesis

GMP may be prepared (a) from 2′,3′-*O*-isopropylideneguanosine by phosphorylation with $POCl_3$,[2964] $P_2O_3Cl_4$,[2965] phenyl phosphorodichloridate,[2967] or bis(2,2,2-tribromoethyl) phosphorochloridate,[2970] with *p*-nitrophenyl,[2972] 2-cyanoethyl,[3066] or 8-quinolyl[2971] dihydrogen phosphate, or with tetrakis(*p*-nitrophenyl)pyrophosphate[3067]; (b) from 2′,3′-*O*-di(*t*-butyldimethylsilyl)guanosine by phosphorylation with diallyl phosphorochloridate,[2969] or (c) from unprotected guanosine by phosphorylation with $POCl_3$,[2976] $P_2O_3Cl_4$,[3068] or bis(2-*t*-butylphenyl) phosphorochloridate.[2977]

GDP may be prepared (a) from 5′-*O*-tosylguanosine by reaction with tris(tetra-*n*-butylammonium) pyrophosphate,[2981] (b) from GMP by condensation with phosphoric acid in the presence of DCC[3069] or 1,1′-carbonyldiimidazole,[2983] (c) from GMP by reaction with benzyl hydrogen phosphoramidate[3070] or phosphoric triimidazolide,[2987] (d) from guanosine 5′-phosphoramidate by reaction with anhydrous phosphoric acid,[3071] or (e) from a GMP anhydride by displacement with tri-*n*-butylammonium phosphate.[2989,3010]

GTP may be prepared (a) from GMP by condensation with phosphoric acid in the presence of DCC[3069] or 1,1′-carbonyldi(2-methylimidazole)[1756] or with tri-*n*-butylammonium pyrophosphate in the presence of 1,1′-carbonyldiimidazole,[3072] (b) from GMP by phosphorylation with phosphoric triimidazolide,[2987] (c) from GMP by enzymatic phosphorylation PEP, pyruvate kinase, and guanylate kinase in the presence of a catalytic amount of ATP,[3072] or (d) from a GMP anhydride,[2989] ester,[3012] or morpholide[3073] by displacement with bis(tri-*n*-butylammonium) pyrophosphate.

## Hydrolysis

Hydrolysis of GMP with 5% $H_2SO_4$ is essentially complete within 30 min at 100 °C, yielding a mixture of guanine (96.2%), guanosine (1.2%), ribose (65.6%), ribose phosphate (32.7%), and $P_i$ (68.0%). Based on these results and a separate determination of the behavior of each product under identical conditions, Ishikawa concludes that the principal reaction is glycolytic cleavage of the GMP to guanine and ribose phosphate.[3018] At intermediate pHs (5-9), GMP is hydrolyzed to guanosine and $P_i$ in the same manner as AMP but at a somewhat faster rate,[3013] and is also subject to catalysis under mild conditions by Ce (III) and other heavy metal ions[3015] and by lanthanide complexes.[3016]

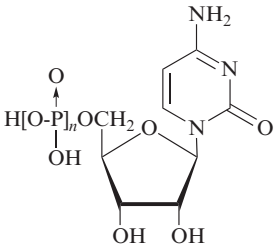
The behavior of GDP toward hydrolysis with $NaClO_4$ ($10^{-3}M$, $I=0.1$, 50 °C) parallels that of ADP, the rate decreasing with increasing pH and independent of the kind of nucleic base. The hydrolysis is significantly accelerated by Cu(II), passing through a pH optimum at 6.0 where the Cu(II) interaction is strongest.[3074]

Hydrolysis of GTP over the pH range 2-10 parallels that of ATP, and is likewise catalyzed by Cu(II) though weaker at its maximum (pH 6.2) by a factor of 2.[3074] The hydrolysis is also catalyzed by Ce(III) and Th(IV).[3022]

### Phosphorylation

Methods for the phosphorylation of GMP to GDP or GTP are discussed under the section "Synthesis" above. These methods, which result in an extension of the phosphate chain, employ either a phosphorylating agent containing a reactive P—Cl, P—N, or P—O bond or a condensing agent to link a $P_i$ to the terminal phosphate group. The reaction of GMP with sodium trimetaphosphate, however, takes a different course, giving a 1:1 mixture of 2′,5′-GDP and 3′,5′-GDP, products of phosphorylation of the two remaining ribose ring OH groups.[3029]

## Cytidine Phosphates




CMP, $n = 1$
CDP, $n = 2$
CTP, $n = 3$

### Physical Properties

Cytidine 5′-Phosphate (CMP), $C_9H_{14}N_3O_8P$. *5′-Cytidylic Acid.*

CMP [63-37-6]: Dense white monoclinic wedge-shaped crystals[3075] or elongated plates (photo),[2907] mp 227 °C,[3075] 230 °C[3076] or dec. 230-233 °C (sealed tube),[2907] $[\alpha]_D^{20} + 49.1°(H_2O)$[3076] or +23.43° (0.5*N* NaOH),[3075] $[\alpha]_D^{25} + 26.0°$(10% HCl) or +25.5° (2% NaOH),[2907] $[\alpha]_D^{50} + 47.5°(H_2O)$[2907]; fluorescence,[3077] phosphorescence,[3033] hydrophobicity,[2857] countercurrent distribution,[2856] polarographic reduction.[3078] Ionization constants: p$K_a$ 0.80, 4.24, 5.97, ~13.2 (potentiometric, 25 °C),[2861] 4.5, 6.3 (UV, 25 °C).[2862] Spectra: UV (fig.),[2864] IR,[3079] far IR (fig.),[3080] FTIR (fig.),[3081] Raman (fig.),[3082] ORD (fig.),[3042] CD (fig.),[3043] [$^1$H] NMR,[3083] [$^{13}$C] NMR,[2946] [$^{31}$P] NMR,[68] 2d-[$^1$H] NMR (fig.),[3084] FD-MS,[3085] EI-MS (TMS derivative),[2883] FAB-MS/MS,[2890] ultrasound.[3047] piezoelectric resonance (fig.).[3086] Chromatography: PC,[9] TLC,[3049] HPTLC,[2891] IEC,[2894] HPLC,[2440] GC (etheno derivative),[3087] column (activated carbon),[2896] GFC.[2893] Electrophoresis: PE,[9] TLE,[3050] isotachophoresis,[2897] CZE,[2900] MEKC.[2901]

$Li_2C_9H_{12}N_3O_8P$ [R.N. 19326-12-6]: $[\alpha]_D$ +6.9° ($H_2O$).[3088]

$NaC_9H_{13}N_3O_8P$ [R.N. 3106-19-2]: FAB-MS/MS.[2890]

$Na_2C_9H_{12}N_3O_8P$ [R.N. 6757-06-8]: Long orthorhombic needles, $d_m$ 1.622, $d_c$ 1.581, X-ray structure[3089]; IR (fig.),[3090] FAB-MS.[2911] *Tetrahydrate*: Raman (fig.).[3041]

$BaC_9H_{12}N_3O_8P{\cdot}8.5H_2O$: Long, thin orthorhombic needles, $d_m$ 1.845, $d_c$ 1.844, X-ray structure.[3091] *Anhydrous* [R.N. 13435-44-4]: $[\alpha]_D^{20} + 14.0°(H_2O)$.[3092]

$(C_{23}H_{26}N_2O_4)_2C_9H_{14}N_3O_8P$ (brucine salt): Crystalline solid, mp 180-182 °C, soluble in hot ethanol, insoluble in water.[3075]

Cytidine 5′-Diphosphate (CDP), $C_9H_{15}N_3O_{11}P_2$. *Cytidine 5′-(Trihydrogen Diphosphate)*.

CDP [63-38-7]: Needles (photo)[2932]; bioluminescence,[2860] liquid-liquid extraction,[2919] countercurrent distribution,[2856] polarographic reduction.[3035] Ionization constants: p$K_a$ 7.18 (potentiometric, 25 °C),[3062] 4.6, 6.4 (UV, 25 °C).[2862] Spectra: UV (fig.),[2864] [$^1$H] NMR,[461] [$^{31}$P] NMR,[68] tunneling (fig.),[2872] ultrasound (fig.).[3093] Chromatography: PC,[9] HPTLC,[2891] IEC,[2770] HPLC,[2440] GFC.[2930] Electrophoresis: PE,[9] CZE,[2900] isotachophoresis,[2897] MEKC.[2901] *Monohydrate*: Air-stable, $d_m$ 1.745, $d_c$ 1.749, X-ray structure.[3094]

Cytidine 5′-Triphosphate (CTP), $C_9H_{16}N_3O_{14}P_3$. *Cytidine 5′-(Tetrahydrogen Triphosphate)*.

CTP [65-47-4]: Bioluminescence,[2860] liquid-liquid extraction,[2919] countercurrent distribution,[2856] polarographic reduction.[3035] Ionization constants: p$K_a$ 7.65 (potentiometric, 25 °C),[3062] 4.8, 6.6 (UV, 25 °C).[2862] Spectra: UV (fig.),[2862] [$^1$H] NMR (fig.),[3072] [$^{31}$P] NMR,[68] ultrasound (fig.),[3093] FD-MS.[3095] Chromatography: PC,[9] HPTLC,[2891] IEC,[2894] HPLC,[2440] GFC.[2930] Electrophoresis: PE,[9] CZE,[2900] isotachophoresis,[2897] MEKC.[2901]

$Na_2C_9H_{14}N_3O_{14}P_3$ [R.N. 36051-68-0]: ES-MS.[2954]

$Na_4C_9H_{12}N_3O_{14}P_3$: White nonhygroscopic water-soluble powder.[3096]

## Conformation

The conformation of CMP in the solid state and in aqueous solution is similar to that of AMP, based on X-ray analysis of the barium salt[3091] and on $^1$H and $^{13}$C NMR spectroscopic analysis of the sodium salt in neutral aqueous solution.[3097,3098] The C(4′)—C(5′) bond and *anti* conformation of CMP are preserved in CDP. The diphosphate group is oriented toward the ribose hydroxyl groups in CDP but away from them in CDP-choline.[3094]

## Synthesis

CMP may be prepared (a) by phosphorylation of 2′,3′-*O*-isopropylidenecytidine with $POCl_3$[2964] or $P_2O_3Cl_4$,[2965] with diallyl[2969] or dibenzyl[376] phosphorochloridate, with *p*-nitrophenyl[2972] or 8-quinolyl[2971] dihydrogen phosphate, or with $H_3PO_4/P_2O_5$[3071]; (b) by phosphorylation of unprotected cytidine with $POCl_3$,[2976] $P_2O_3Cl_4$,[3068] or di(2-*t*-butylphenyl) phosphorochloridate,[2977] or (c) by fusion of 2,3-di-*O*-benzoyl-5-(diphenylphosphonooxy)-D-ribofuranosyl bromide with bis(trimethylsilyl)-*N*-acetylcytosine[3088] or trimethylsilyl 4-ethoxy-2(1*H*)-pyrimidinone.[2980]

CDP may be prepared (a) from 5′-*O*-tosylcytidine by reaction with tris(tetra-*n*-butylammonium)pyrophosphate[2981]; (b) from CMP by phosphorylation with phosphoric triimidazolide,[2987] 2-cyanoethyl-α-pyridyl phosphate,[2988] or benzyl dihydrogen phosphate,[3099] (c) from cytidine 5′-phosphoramidate[3071] or 5′-phosphoromorpholidate[3007] and anhydrous phosphoric acid, (d) by displacement of diphenyl phosphate[3010] or

di-*n*-butylphosphinothioic acid[2989] from a CMP anhydride or of α-pyridone or 8-hydroxyquinoline from a CMP ester by reaction with tri-*n*-butylammonium phosphate.

CTP may be prepared (a) from CMP by phosphorylation with phosphoric triimidazolide,[2987] (b) from CMP by enzymatic phosphorylation with PEP in the presence of pyruvate kinase and adenylate kinase,[3072] (c) from CMP by condensation with tri-*n*-butylammonium pyrophosphate in the presence of 1,1′-carbonyldiimidazole,[3072] or (d) from a CMP anhydride,[2989] ester,[3012] amidate,[3006] or morpholidate[3096] by displacement with bis(triethylammonium) or bis(tri-*n*-butylammonium) pyrophosphate.

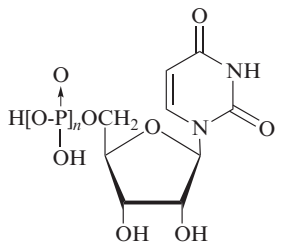
### Hydrolysis

Hydrolysis of CMP with 10% sulfuric acid at 125 °C gives cytidine, isolated as the picrate.[3092] Almost no effect is observed when aqueous solutions of CMP are heated at 100 °C under various pH conditions.[3100]

### Phosphorylation

Methods for the phosphorylation of CMP to CDP or CTP are discussed under the section "Synthesis" above. These methods, which result in an extension of the phosphate chain, employ either a phosphorylating agent containing a reactive P—Cl, P—N, or P—O bond or a condensing agent to link $P_i$ to the terminal phosphate group. The reaction of CMP with sodium trimetaphosphate, however, takes a different course giving a 1:1 mixture of 2′,5′-CDP and 3′,5′-CDP, products of phosphorylation of the two remaining ribose ring OH groups, after 48 days at room temperature.[3029]

## Uridine Phosphates




UMP, $n = 1$
UDP, $n = 2$
UTP, $n = 3$

### Physical Properties

Uridine 5′-Phosphate (UMP), $C_9H_{13}N_2O_9P$. *5′-Uridylic Acid*

UMP [R.N. 58-97-9]: Elongated prisms with pointed ends,[2907] mp 202 °C (sealed capillary),[3101] $[\alpha]_D^{20} + 10.5°$ ($H_2O$),[3101] +11.1° ($H_2O$),[3076] or +6.5° (2% NaOH)[2907]; $[\alpha]_D^{28} + 3.44$ (10% HCl)[3102]; fluorescence,[3077] phosphorescence,[3033] polarographic reduction.[3035] Ionization constants: p$K_a$ 1.02, 5.88, 9.43, ~13.9 (potentiometric, 25 °C),[2861] 6.4, 9.5 (UV, 25 °C).[2862] Spectra: UV (fig.),[2864] IR (fig.),[3103] ORD (fig.),[3042] CD (fig.),[3043] [$^1$H] NMR (fig.),[3097] [$^{13}$C] NMR (fig.),[3105] [$^{31}$P] NMR,[68] 2d-[$^{13}$C,$^{31}$P] NMR (fig.),[2882] EI-MS (TMS derivative),[2883] FD-MS,[3085] EH-MS,[2888] tunneling (fig.),[2872] ultrasound.[2873] Chromatography: PC,[9] TLC,[36] HPTLC,[2891] IEC,[2894] HPLC,[2440] GC (TMS derivative),[2892]

GFC,[2893] column (activated carbon).[2896] Electrophoresis: PE,[32] TLE,[36] CZE,[3106] isotachophoresis,[2897] MEKC.[2901] Theoretical calculations: PCILO,[2902] CNDO.[3052]

$Na_2C_9H_{11}N_2O_9P{\cdot}7H_2O$ [R.N. 64426-16-0]: Orthorhombic crystals, $d_m$ 1.64, $d_c$ 1.64, X-ray structure.[3107] Spectra: IR (fig.),[3103] Raman,[2910] FT Raman (fig.),[3108] laser Raman (fig.),[3109] FAB-MS.[2911]

$BaC_9H_{11}N_2O_9P$ [3486-23-5]: Long needles (photo).[3110] *Dihydrate*: Amorphous solid, IR (fig.).[3103] *Nonahydrate*: Platelike crystals, $d_m$ 2.05, X-ray structure[3111]; laser Raman (fig.).[3109]

$NH_3C_9H_{13}N_2O_9P$: Prismatic needles (photo), s. 200 °C, dec. 242 °C (sealed tube), $[\alpha]_D^{50} + 10.5°(H_2O)$,[2907] $[\alpha]_D^{20} + 13.0°(H_2O)$,[3112] +1.5° (2% NaOH),[2907] $[\alpha]_D^{25} + 2.5°$(10% HCl).[2907]

$(NH_3)_2C_9H_{13}N_2O_9P$: Heavy elongated prisms, dec. 185 °C, $[\alpha]_D^{20} + 21.0°(H_2O)$,[3112] +21.9° ($H_2O$).[3076]

$(C_{23}H_{26}N_2O_4)_2C_9H_{13}N_2O_9P{\cdot}3.5H_2O$ (brucine salt) [R.N. 21145-59-5]: Colorless needles, s. 170 °C, dec. 229-232 °C,[2980] $[\alpha]_D^{18} - 70.4°$ (pyridine).[376]

### Uridine 5′-Diphosphate (UDP), $C_9H_{14}N_2O_{12}P_2$. *Uridine 5-(Trihydrogen Diphosphate)*

UDP [R.N. 58-98-0]: Crystalline solid, very stable in alkaline solution[2770]; bioluminescence,[2860] liquid-liquid extraction,[2919] countercurrent distribution.[2856] Ionization constants: p$K_a$ 7.16 (potentiometric, 25 °C),[3062] 6.5, 9.4 (UV, 25 °C).[2862] Spectra: UV (fig.),[2864] [$^1$H] NMR,[461] [$^{31}$P] NMR.[68] Chromatography: PC,[9] TLC,[36] HPTLC,[2891] IEC,[2770] HPLC,[2440] GFC.[2930] Electrophoresis: PE,[9] TLE,[36] CZE,[3106] isotachophoresis,[2897] MEKC.[2901]

$K_2C_9H_{12}N_2O_{12}P_2{\cdot}3H_2O$ [R.N. 71229-83-9]: Flat orthorhombic plates, $d_x$ 1.84, X-ray structure.[3113]

### Uridine 5′-Triphosphate (UTP), $C_9H_{15}N_2O_{15}P_3$. *Uridine 5′-(Tetrahydrogen Triphosphate)*

UTP [R.N. 63-39-8]: Bioluminescence,[2860] liquid-liquid extraction,[2919] countercurrent distribution,[2856] polarographic reduction.[3035] Ionization constants: p$K_a$ 7.58, 9.5 (potentiometric, 25 °C),[3062,3064] 2.86, 4.05, 6.72 (potentiometric, 35 °C),[3114] 6.6, 9.5 (UV, 25 °C).[2862] Spectra: UV (fig.),[2862] Raman (fig.),[3115] [$^{31}$P] NMR.[68] Chromatography: PC,[9] TLC,[36] HPTLC,[2891] IEC,[2894] HPLC,[2440] GFC.[2930] Electrophoresis: PE,[32] TLE,[36] CZE,[2900] isotachophoresis,[2897] MEKC.[2901]

$Na_3C_9H_{12}N_2O_{15}P_3$ [R.N. 19817-92-6]: ES-MS,[2954] SI-MS,[3116] thermospray MS.[3117]

## Conformation

The conformation of UMP in the solid state, based on X-ray analysis of the disodium[3107] and barium[3111] salts, is similar to that of AMP; the preferred conformation is *anti* C(2′)-endo gg.[3107] The *anti* and gg conformations are both stabilized by the electrostatic attractive interactions between the 5′-phosphate group and the pyrimidine base.[3118] The conformation of UMP in aqueous solution, based on $^1$H and $^{13}$C NMR analysis, is not significantly different from that of the crystalline salt.[3097,3098]

## Synthesis

UMP may be prepared (a) by phosphorylation of 2′,3′-*O*-isopropylideneuridine with $POCl_3$[2964] or $P_2O_3Cl_4$,[2965] with diallyl[2969] or dibenzyl[376] phosphorochloridate, with *p*-nitrophenyl[2972] or 8-quinolyl[2971] dihydrogen phosphate, with tris(8-quinolyl)phosphate,[3119] or with $H_3PO_4$-$P_2O_5$,[2986] (b) by phosphorylation of 2′,3′-*O*-benzylideneuridine with diphenyl[3120] or dibenzyl[3121] phosphorochloridate, (c) by phosphorylation of unprotected uridine with $POCl_3$,[2976] $P_2O_3Cl_4$,[3068] or tris(8-quinolyl)phosphate,[2978] (d) by fusion of 2,3-di-*O*-benzoyl-5-(diphenylphosphonooxy)-D-ribofuranosyl bromide with bis(trimethylsilyl)uracil,[2980] or (e) by deamination of CMP.[3122]

UDP may be prepared (a) from 5′-*O*-tosyluridine by reaction with tris(tetra-*n*-butylammonium)pyrophosphate[2981]; (b) from UMP by phosphorylation with dibenzyl phosphorochloridate,[2986] phosphoric triimidazolide,[2987] 2-cyanoethyl α-pyridyl phosphate,[2988] or ethoxyvinyl dibenzyl phosphate[3123]; (c) from uridine 5′-phosphoramidate[3124] or 5′-phosphoromorpholidate[3007] by condensation with anhydrous phosphoric acid or tri-*n*-butylammonium phosphate; (d) from a UMP anhydride by reaction with tri-*n*-butylammonium phosphate[2989]; or (e) from other UMP derivatives containing protecting substituents at the 2′-OH and 3′-OH positions.[2995,3125]

UTP may be prepared (a) from UMP by phosphorylation with phosphoric triimidazolide,[2987] (b) from UMP by enzymatic phosphorylation with PEP in the presence of pyruvate kinase and adenylate kinase,[3072] (c) from UMP by condensation with phosphoric acid in the presence of DCC[3126] or with tri-*n*-butylammonium pyrophosphate in the presence of 1,1′-carbonyldiimidazole,[3072] or (d) from a UMP anhydride,[2989,3010] ester,[3012] or amidate[3006] by displacement with bis-(triethylammonium) or bis(tri-*n*-butylammonium)pyrophosphate, (e) from various other UMP derivatives containing protecting substituents at the 2′-OH and 3′-OH positions,[2995,3127] or (f) from CTP by deamination with sodium nitrite.[3072]

## Hydrolysis

The hydrolysis of UTP over the pH range 2-10 parallels that of ATP, GTP, and CTP. Its behavior toward Cu(II) and other metal ion catalysts differs from that of ATP and GTP owing to the absence of metal ion-pyrimidine interaction, but the rate of hydrolysis is significantly enhanced if the Cu(II) to UTP ratio is raised from 1:1 to 2:1. The reactivity of the metal ion decreases in the order Cu > Ni > Zn.[3128]

## Phosphorylation

Methods for the phosphorylation of UMP to UDP or UTP are discussed under the section "Synthesis" above. These methods, which result in an extension of the phosphate chain, employ either a phosphorylating agent containing a reactive P—Cl, P—N, or P—O bond or a condensing agent to link a $P_i$ to the terminal phosphate group. The reaction of UMP with sodium trimetaphosphate, however, can take a different course, depending on the reaction conditions. It gives either a mixture of uridine 5′-polyphosphates $P_nU$, where U = uridine and $n = 4$, 7, and 10,[3030] or a 1:1 mixture of 2′,5′-ADP and 3′,5′-ADP, products of phosphorylation of the remaining free OH groups of the ribose ring.[3029]

**Table 5-3** Deoxyribonucleotides in Plants

| No. | Plant part | Method | dADP | dATP | dGDP | dGTP | dCDP | dCTP | TDP | TTP | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acer pseudoplatanus* L. (Sycamore Maple) | | | | | | | | | | | |
| 1 | Callus culture[a] | TLC | | 3.3 | | 2.3 | | 0.6 | | 2.0 | 2434 |
| *Lycopersicon esculentum* L. (Tomato) | | | | | | | | | | | |
| 1 | Root tip | HPLC | 2.67 | 5.40 | 0.68 | 8.41 | 0.97 | 4.31 | 3.12 | 2.81 | 2435 |
| *Nicotiana tabacum* L. (Tobacco) | | | | | | | | | | | |
| 1 | Callus culture[a] | TLC | | 51.3 | | 4.3 | | 5.8 | | 6.8 | 2434 |
| *Pinus mugo* Turra (Mugo Pine) | | | | | | | | | | | |
| 1 | Pollen[a] | TLC | | 2.0 | | 2.0 | | 3.3 | | 2.8 | 2434 |
| *Vicia faba* L. (Faba Bean) | | | | | | | | | | | |
| 1 | Root tip[b] | FFL | | 51 | | | | | | | 3129 |

nmol/g fwb unless stated otherwise.
[a]Dry weight basis.
[b]nmol/20 root tips.

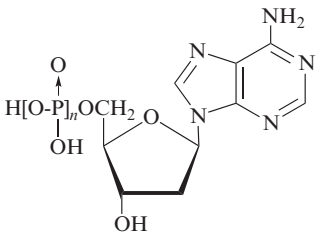
# DEOXYRIBONUCLEOTIDES

This group comprises the adenosine derivatives dAMP, dADP, and dATP; the guanosine derivatives dGMP, dGDP, and dGTP; the cytidine derivatives dCMP, dCDP, and dCTP; the uridine derivatives dUMP, dUDP, and dUTP; and the thymidine derivatives TMP, TDP, and TTP (Y = H in the formula on p 289).

## Extraction, Separation, and Analysis

The deoxyribonucleotides are extracted together with the ribonucleotides by ice-cold 0.3*M* perchloric acid[2434] or 6% trichloroacetic acid.[2435] Because of the disparity in concentration levels between the two classes of compounds, it is advisable to destroy the latter by treatment of the extract with periodate prior to analysis.[2435,3129] The deoxyribonucleotides may be separated by two-dimensional TLC or HPLC and analyzed by UV,[2435] by $^{32}P$ labeling,[2434] or by the firefly luminescence (FFL) method.[3130] The results are shown in Table 5-3.

# Deoxyadenosine Phosphates




dAMP, $n = 1$
dADP, $n = 2$
dATP, $n = 3$

## Physical Properties

2′-Deoxyadenosine 5′-Phosphate (dAMP), $C_{10}H_{14}N_5O_6P$. Beilstein **26**, $E_{IV}$ 3591-2. *2′-Deoxy-5′-Adenylic Acid*

dAMP [R.N. 653-63-4]: Plates (from water),[3131] mp 142.5 °C,[3132] hydrophobicity,[2857] phosphorescence,[3133] liquid-liquid distribution coefficient[3134]; DC[3135] and AC[3136] polarographic reduction; conformation in solution.[3097] Ionization constants: p$K_a$ ~4.4, 6.4 (potentiometric),[3137] 3.79 (UV, 20 °C),[3138] 6.65 (thermometric, 25 °C).[3139] Themodynamics: N–H ionization,[3140] PO–H ionization,[3139] theoretical calculation.[3141] Spectra: UV (fig.),[3043] far UV,[365] Raman (fig.),[3142] UV Raman (fig.),[3143] ORD (fig.),[3042] CD (fig.),[3043] [$^1$H] NMR (fig.),[2875] [$^{13}$C] NMR (fig.),[2946] [$^{31}$P] NMR,[3144] ultrasound.[3047] Mass spectra: EI,[3145] FAB,[3146] ESI,[3147] PD,[3148] CID.[3149] Chromatography: PC,[3150] TLC,[3049] HPTLC,[3151] IEC,[3151] HPLC (ion exchange,[3152] ion pairing,[3153] ion suppression,[3154] reversed phase[3155]), GC,[3156] GFC,[3157] CC (activated carbon),[2896] MEKC.[3158] Electrophoresis: PE,[3159,3160] TLE,[3161] CZE,[3162] CE.[3163] Theoretical calculations: Extended Hückel,[3164] Hartree-Fock,[3165,3166] CNDO,[3052] *ab initio* SCF,[3167] PCILO.[2902]
$NaC_{10}H_{13}N_5O_6P{\cdot}6H_2O$ [R.N. 39925-66-1]: Orthorhombic crystals, $d_m$ 1.53, $d_c$ 1.511, X-ray structure.[3168] [$^{23}$Na] NMR,[3169] HF-CO,[3165] XANES (fig.).[3170]
$CaC_{10}H_{12}N_5O_6P$: Crystals (fig.),[3171] $[\alpha]_D^{19} - 38°(H_2O)$,[3131] Raman,[3172] HF-CO.[3166]
*Pentahydrate*: [R.N. 90550-55-3]: Colorless orthorhombic plates, $d_c$ 1.697, X-ray structure.[3173]

2′-Deoxyadenosine 5′-Diphosphate (dADP), $C_{10}H_{15}N_5O_9P_2$. *2′-Deoxyadenosine 5′-(Trihydrogen Diphosphate)*

dADP [R.N. 2793-06-8]: AC Polarography.[3136] Chromatography: PC,[3025] TLC,[3174] IEC,[3175] HPLC (anion exchange,[2435] reversed phase,[3176] ion pairing[3177]). Electrophoresis: PE,[3178] CE.[3163]

2′-Deoxyadenosine 5′-Triphosphate (dATP), $C_{10}H_{16}N_5O_{12}P_3$. *2′-Deoxyadenosine 5′-(Tetrahydrogen Triphosphate)*

dATP [R.N. 1927-31-7]: Countercurrent distribution,[2856] bioluminescence,[2860] AC polarography,[3136] p$K_a$ 3.9, 7.0 (potentiometric, 70 °C).[3179] Spectra: UV,[3180] Raman,[3181] $^1$H NMR,[3180] $^{31}$P NMR,[3182] EI-MS (TMS derivative),[3183] FAB-MS,[3184] MALDI-MS,[3184] PD-MS.[3185] Chromatography: PC,[3025] TLC,[3049] IEC,[3175] HPLC (anion exchange,[2435] reversed phase,[3176] ion pairing [3177]), CC.[3180] Electrophoresis: PE,[3006] CE,[3163] CZE.[3186]
$Na_4C_{10}H_{12}N_5O_{12}P_3{\cdot}3H_2O$: White nonhygroscopic water-soluble powder.[3096]

## Conformation

The conformation of dADP, like that of ADP, is extended rather than folded in aqueous solution. The ribose is predominantly $^2$E and the base has only a small *syn* contribution, as determined by NMR spectroscopy.[2960]

## Synthesis

dAMP may be prepared by phosphorylation (a) of 3′-acetyl-2′-deoxyadenosine with dibenzyl phosphorochloridate,[3187] (b) of *N*-benzoyl-3′-DMT-2′-deoxyadenosine with

phosphoryl tris(triazolide),[3188] or (c) of unprotected 2′-deoxyadenosine with $POCl_3$ in trimethyl phosphate.[3189] Treatment of 2′-deoxyadenosine with monoammonium phosphate in formamide under simulated prebiotic conditions (several weeks at 37 °C) yields predominantly 5′-dAMP, together with 3′-dAMP and other by-products. The yield of 5′-dAMP was 21%, compared to 19%, 26%, and 10% for 5′-dGMP, dCMP, and TMP, respectively.[3190] For the effect of reaction temperatures varying from 25 °C to 140 °C on these reactions, see Schoffstall *et al.*[3031]

dADP may be prepared (a) by condensation of a dAMP amidate,[3191] imidazolidate,[3188] or anhydride[3178] with tri-*n*-butylammonium phosphate or (b) by enzymatic phosphorylation of dAMP with ATP.[3192]

dATP may be prepared (a) by phosphorylation of 2′-deoxyadenosine with $POCl_3$ in trimethyl phosphate followed by reaction with bis(tri-*n*-butylammonium)pyrophosphate,[3000] (b) by condensation of a dAMP amidate,[3006,3191] imidazolidate,[3180,3193] or morpholidate[3096] with bis(tri-*n*-butylammonium)pyrophosphate, or (c) by enzymatic phosphorylation of dAMP or dADP with ATP.[3192,3194] Phosphorylation of 2′-deoxyadenosine with sodium trimetaphosphate yields predominantly 3′-dATP.[3195]

## Hydrolysis

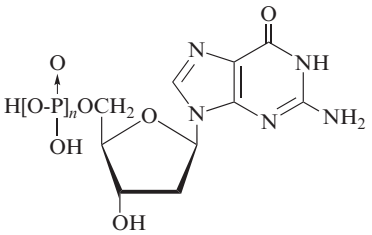
dAMP is resistant to hydrolysis under neutral or basic conditions but is readily split by acid, giving adenine and 2-deoxyribose-5-phosphate.[3196,3197] The rate constant $k$ is $15.4 \times 10^{-4}\ s^{-1}$ in 0.001*M* HCl at 363.2°K, less than half the $32.0 \times 10^{-4}\ s^{-1}$ rate constant for 2′-deoxyadenosine.[3198] In contrast, hydrolysis of dAMP in the presence of a Ce(IV) catalyst cleaves the phosphate ester bond under neutral conditions (pH 7.2, 50 °C) giving 2′-deoxyadenosine.[3199] The pseudo-first-order rate constant $k$ is $6.7 \times 10^{-4}\ min^{-1}$. This hydrolysis can also be performed under basic conditions if cyclodextrin is added to suppress the formation of cerium hydroxide gels.[3200]

The hydrolysis of dADP to dAMP in aqueous solution (70 °C, $I = 0.2$) is first order with respect to dADP and is acid catalyzed, the rate constant $k$ decreasing from $10.7 \times 10^{-6}\ s^{-1}$ at pH 5 to $0.4 \times 10^{-6}\ s^{-1}$ at pH 8.5,[3179] paralleling that of ADP in this pH range.[3027] Likewise, the acid-catalyzed hydrolysis of dATP to dADP under the same conditions is first order with respect to dATP, the rate constant $k$ decreasing from $10.4 \times 10^{-6}\ s^{-1}$ at pH 5.1 to $0.9 \times 10^{-6}\ s^{-1}$ at pH 8.5,[3179] paralleling that of ATP in this pH range.[3027] At pH 4 and below, however, rapid cleavage of the *N*-glycosidic bond occurs in both cases owing to the inherent sensitivity of 2′-deoxyadenosine to acid; 2′,3′-dideoxyadenosine is even more acid-sensitive.[3179]

## Phosphorylation

Methods for the phosphorylation of dAMP to dADP or dATP are described under the section "Synthesis" above. dAMP is unaffected by sodium trimetaphosphate, a reagent that readily phosphorylates AMP.[3029]

# Deoxyguanosine Phosphates



dGMP, $n = 1$
dGDP, $n = 2$
dGTP, $n = 3$

## Physical Properties

2′-Deoxyguanosine 5′-Phosphate (dGMP), $C_{10}H_{14}N_5O_7P$. Beilstein **26**, $E_{IV}$ 3899-900. *2′-Deoxy-5′-Guanylic Acid*

dGMP [R.N. 902-04-5]: Long needles (fig.),[3171,3201] mp 180-182 °C[3137]; phosphorescence,[3133] chemiluminescence,[3034] liquid-liquid distribution coefficient,[3134] lactim-lactam tautomerism,[3036] conformation in solution.[3097] Ionization constants: p$K_a$ 2.9, 6.4, 9.7 (potentiometric),[3137] 9.33 (UV, 20 °C),[3138] 6.87 ($^{31}$P NMR, 27 °C)[3202]; thermodynamics of N–H ionization.[3140] Spectra: UV (fig.),[3043] far UV,[365] FTIR (fig.),[2909] Raman (fig.),[3142] UV Raman (fig.),[3143] ORD (fig.),[3042] CD (fig.),[3043] [$^1$H] NMR,[3203] [$^{13}$C] NMR (fig.),[2946] EI-MS,[3145] ESI-MS,[3147] FAB-MS,[3146] PD-MS,[3148] SI-MS,[3204] CID-MS.[3149] Chromatography: PC,[3150] TLC,[3049] HPTLC,[3151] IEC,[3205] HPLC (ion exchange,[1924] reversed phase,[3155] ion suppression[3154]), CC (activated carbon),[2896] MEKC.[3158] Electrophoresis: PE,[3159] TLE,[3161] CE,[3163] CZE.[3162] Theoretical calculations: Extended Hückel,[3164] Hartree-Fock,[3165] CNDO,[3052] thermodynamics.[3141]
$Na_2C_{10}H_{12}N_5O_7P$: FTIR (fig.),[2909] Raman (fig.),[3041] HF-CO,[3165] XANES (fig.).[3170] *Tetrahydrate* [R.N. 52558-16-4]: Thin monoclinic plates, $d_c$ 1.646,[3206] $d_m$ 1.64,[3207] X-ray structure.[3206]
$BaC_{10}H_{12}N_5O_7P$: Needles, $[\alpha]_D^{19}$ − 31.1°($H_2O$).[3201] *Heptahydrate* [R.N. 133342-19-5]: FTIR, X-ray powder pattern.[3208]

2′-Deoxyguanosine 5′-Diphosphate (dGDP), $C_{10}H_{15}N_5O_{10}P_2$. *2′-Deoxyguanosine 5′-(Trihydrogen Diphosphate)*

dGDP [R.N. 3493-09-2]: Spectra: SI-MS (fig.).[3209] Chromatography: PC,[3025] TLC,[3174] HPLC (anion exchange,[2435] reversed phase,[3176] ion pairing[3177]). Electrophoresis: PE,[3178] CE.[3163]

2′-Deoxyguanosine 5′-Triphosphate (dGTP), $C_{10}H_{16}N_5O_{13}P_3$. *2′-Deoxyguanosine 5′-(Tetrahydrogen Triphosphate)*

dGTP [R.N. 2564-35-4]: Bioluminescence,[2860] countercurrent distribution.[2856] Spectra: UV,[3180] Raman,[3181] [$^1$H] NMR and [$^{31}$P] NMR,[3180] FAB-MS and MALDI-MS.[3184] Chromatography: PC,[3025] TLC,[3049] IEC,[3175] HPLC (anion exchange,[2435] reversed phase,[3176] ion pairing[3177]), CC.[3180] Electrophoresis: CE,[3163] CZE.[3186]
$Na_4C_{10}H_{12}N_5O_{13}P_3 \cdot 3H_2O$: White nonhygroscopic water-soluble powder.[3096]

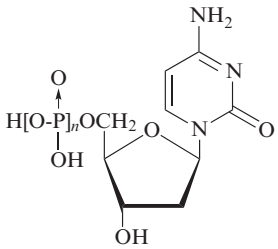
### Synthesis

dGMP may be prepared by phosphorylation (a) of 3′-acetyl-2′-deoxyguanosine with benzylphosphorous diphenylphosphoric anhydride[3187] or (b) of *N*-isobutyryl-3′-DMT-2′-deoxyguanosine with phosphoryl tris(triazolide).[3188] dGDP may be prepared (a) by condensation of a dGMP imidazolide[3188] or anhydride[3178] with tri-*n*-butylammonium phosphate or (b) by enzymatic phosphorylation of dGMP with UTP.[3192] dGTP may be prepared (a) by condensation of a dGMP imidazolidate[3180,3193] or morpholidate[3096] with bis(tri-*n*-butylammonium)pyrophosphate or (b) by enzymatic phosphorylation of dGDP with UTP.[3192] Phosphorylation of 2′-deoxyguanosine with sodium trimetaphosphate yields predominantly 3′-dGTP.[3195]

### Hydrolysis

dGMP is resistant to hydrolysis under neutral or basic conditions but is readily split by acid, giving guanosine and 2-deoxyribose-5-phosphate.[3196,3197] Under neutral conditions (pH 7.2, 50 °C), however, hydrolysis in the presence of $CeCl_3$ cleaves the P—O bond giving 2′-deoxyguanosine. The rate constant $k$ is $2.8 \times 10^{-2}$ $min^{-1}$.[3199]

## Deoxycytidine Phosphates




dCMP, $n = 1$
dCDP, $n = 2$
dCTP, $n = 3$

### Physical Properties

2′-Deoxycytidine 5′-Phosphate (dCMP), $C_9H_{14}N_3O_7P$. Beilstein **25**, $E_{IV}$ 3664.
*2′-Deoxy-5′-Cytidylic Acid*

dCMP [R.N. 1032-65-1]: Long, thin prisms (fig.), mp 183-187 °C dec.[3171] or 185-187 °C,[3132] $[\alpha]_D^{21} + 35°$ ($H_2O$), soluble in water and difficultly soluble in ethanol[3171]; hydrophobicity,[2857] liquid-liquid distribution coefficient,[3134] phosphorescence,[3133] polarographic reduction,[3078] conformation in solution.[3097] Ionization constants: p$K_a$ 4,6, 6.6 (potentiometric),[3137] 4.52 (UV, 25 °C)[3210] thermodynamics of N–H ionization.[3140] Spectra: UV (fig.),[3043] far UV,[365] IR (fig.),[3211] FTIR,[3212] UV Raman (fig.),[3143] ORD (fig.),[3042] CD (fig.),[3043] [$^1$H] NMR,[3213] [$^{13}$C] NMR,[2946] ultrasound,[3047] EI-MS,[3145] EH-MS,[2888] ESI-MS,[3147] FAB-MS,[3146] PD-MS,[3148] SI-MS,[3204] CID-MS.[3149] Chromatography: PC,[3150] TLC,[3049] HPTLC,[3151] IEC,[3211] HPLC (ion exchange,[3152] ion pairing,[3153] ion suppression,[3154] reversed phase[3155]), GFC,[3157] GC-MS,[3214] CC (activated carbon),[2896] MEKC.[3158] Electrophoresis: PE,[3159,3160] TLE,[3161] CZE,[3162] CE.[3163] Theoretical calculations: Atomic charge,[3215] extended Hückel,[3216] Hartree-Fock,[3165] CNDO,[3052] PCILO,[2902] SCF-MO,[3217]

thermodynamics.[3141] *Monohydrate*: Small needles, mp 183-184 °C dec., $[\alpha]_D^{17} + 38.5°(H_2O)$[3211] or colorless monoclininc prisms, $d_m$ 1.687, $d_c$ 1.675, X-ray structure[3218]; dipole moment (calc.) $\mu$ 14.4, $\theta$ 160.[3037] Spectra: Raman (fig.),[3082] ESR.[3219]
$Na_2C_9H_{12}N_3O_7P{\cdot}7H_2O$ [R.N. 85003-63-0]: Orthorhombic crystals, $d_c$ 1.67, X-ray structure[3220]; Raman (fig.)[3041] HF-CO,[3165] XANES (fig.).[3170]
$BaC_9H_{12}N_3O_7P$: $[\alpha]_D^{19} + 14.4°(H_2O)$.[3171]
$CdC_9H_{12}N_3O_7P{\cdot}2H_2O$ [R.N. 90468-86-3]: Orthorhombic crystals, $d_c$ 2.02, X-ray structure[3221]; Raman (fig.).[3041]

2′-Deoxycytidine 5′-Diphosphate (dCDP), $C_9H_{15}N_3O_{10}P_2$. *2′-Deoxycytidine 5′-(Trihydrogen Diphosphate)*

dCDP [R.N. 800-73-7]: Chromatography: PC,[3025] TLC,[3222] IEC,[3223] HPLC (anion exchange,[2435] reversed phase,[3176] ion pairing[3177]). Electrophoresis: CE.[3163]

2′-Deoxycytidine 5′-Triphosphate (dCTP), $C_9H_{16}N_3O_{13}P_3$. *2′-Deoxycytidine 5′-(Tetrahydrogen Triphosphate)*

dCTP [R.N. 2056-98-6]: Countercurrent distribution.[2856] Spectra: UV,[3180] Raman,[3181] [$^1$H] NMR,[3180] [$^{31}$P] NMR,[3180] FAB-MS,[3184] MALDI-MS.[3184] Chromatography: PC,[3025] TLC,[3049] IEC,[3223] HPLC (anion exchange,[2435] reversed phase,[3176] ion pairing[3177]), CC.[3180] Electrophoresis: CE,[3163] CZE.[3186]
$Na_4C_9H_{12}N_3O_{13}P_3{\cdot}H_2O$: White nonhygroscopic water-soluble powder.[3096]

## Synthesis

dCMP may be prepared by phosphorylation (a) of *N*,3′-diacetyl-2′-deoxycytidine with dibenzyl phosphorochloridate,[3211] (b) of *N*-benzoyl-3′-DMT-2′-deoxycytidine with phosphoryl tris(triazolide),[3188] or (c) of unprotected 2′-deoxycytidine with $POCl_3$ in trimethyl phosphate.[3189]

dCDP may be prepared (a) by condensation of a dCMP imidazolidate[3188] or anhydride[3178] with tri-*n*-butylammonium phosphate or (b) by enzymatic phosphorylation of dCMP with ATP.[3192]

dCTP may be prepared (a) by condensation of a dCMP imidazolidate[3180,3193] or morpholidate[3096] with bis(tri-*n*-butylammonium) pyrophosphate or (b) by enzymatic phosphorylation of dCDP with ATP.[3192] Phosphorylation of 2′-deoxycytidine with sodium trimetaphosphate yields predominantly 3′-dCTP.[3195]

## Hydrolysis

dCMP is resistant to hydrolysis under neutral or basic conditions but is hydrolyzed upon heating in acid, giving cytosine and 2-deoxyribose-5-phosphate.[3196] The rate increases rapidly in the vicinity of the p*K* of cytosine and then levels off to a plateau; the rate constant *k* at pH 2.1 and 95 °C is $0.610 \times 10^{-4}$ s$^{-1}$ ($\Delta H$, $\Delta S$ given).[3224] In contrast, hydrolysis of dCMP under neutral (pH 7.2, 50 °C) or acid (pH 4.0, 70 °C) conditions in the presence of Ce (IV) or Th(IV) catalyst cleaves the P–O bond giving 2′-deoxycytidine.[3199,3225]

### Phosphorylation

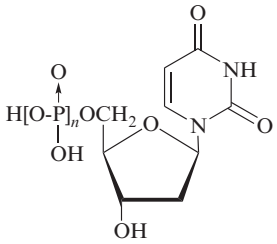
Methods for the phosphorylation of dCMP to dCDP or dCTP are described under the section "Synthesis" above. dCMP is unaffected by sodium trimetaphosphate, a reagent that readily phosphorylates CMP.[3029]

## Deoxyuridine Phosphates

### Physical Properties

2′-Deoxyuridine 5′-Phosphate (dUMP), $C_9H_{13}N_2O_8P$. Beilstein **24**, $E_{IV}$ 1200-01. *2′-Deoxy-5′-uridylic Acid*

dUMP [R.N. 964-26-1]: Finely crystalline hygroscopic solid[3226]; conformation in solution.[3097] Spectra: UV (fig.),[3043] UV Raman (fig.),[3143] CD (fig.),[3043] [$^{13}$C] NMR,[3227] [$^{31}$P] NMR,[3144] EI-MS.[3228] Chromatography: PC,[3150] TLC,[3222] IEC,[3223] HPLC (ion exchange,[3229] ion pairing,[3230] ion suppression,[3154] reversed phase[3231]), GFC.[3157] Electrophoresis: PE,[3226] CE.[3163] Theoretical calculations: CNDO.[3052]




dUMP, $n = 1$
dUDP, $n = 2$
dUTP, $n = 3$

$Na_2C_9H_{11}N_2O_8P{\cdot}5H_2O$ [R.N. 75322-08-6]: Monoclinic crystals, $d_m$ 1.68, $d_c$ 1.64, X-ray structure[3232]; FT Raman (fig.).[3108]

$CdC_9H_{11}N_2O_8P{\cdot}3H_2O$ [R.N. 92484-16-7]: Colorless crystals, $d_c$ 2.14, X-ray structure.[3233]

2′-Deoxyuridine 5′-Diphosphate (dUDP), $C_9H_{14}N_2O_{11}P_2$. *2′-Deoxyuridine 5′-(Trihydrogen Diphosphate)*

dUDP [R.N. 4208-67-7]: Chromatography: PC,[3150] HPLC (reversed phase,[3176] ion pairing).[3177] Electrophoresis: CE.[3163]

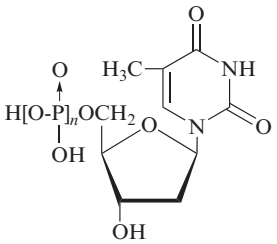
2′-Deoxyuridine 5′-Triphosphate (dUTP), $C_9H_{15}N_2O_{14}P_3$. *2′-Deoxyuridine 5′-(Tetrahydrogen Triphosphate)*

dUTP [R.N. 1173-82-6]: Bioluminescence.[2860] Chromatography: PC,[3150] TLC,[3222] HPLC (reversed phase),[3176] IC.[3234] Electrophoresis: CE.[3163]

### Synthesis

dUMP may be prepared (a) by phosphorylation of 3′-acetyl-2′-deoxyuridine with dibenzyl phosphorochloridate or tetra-*p*-nitrophenyl pyrophosphate,[3226] (b) by phosphorylation of unprotected 2′-deoxyuridine with $POCl_3$ in trimethyl phosphate,[3189] (c) by hydrolysis of 2′-deoxyuridine 5′-phosphorodiamidate,[3235] or (d) by deamination of dCMP with nitrous acid.[3236]

# Thymidine Phosphates




TMP, $n = 1$
TDP, $n = 2$
TTP, $n = 3$

## Physical Properties

Thymidine 5′-Phosphate (TMP), $C_{10}H_{15}N_2O_8P$. Beilstein **24**, $E_{IV}$ 1301-02.
*5′-Thymidylic Acid*

TMP [R.N. 365-07-1]: Microcrystalline solid, soluble in water and dilute ethanol,[3171] $[\alpha]_D$ −12.3° (HCl)[3088] hydrophobicity,[2857] fluorescence,[3077] phosphorescence,[3033,3133] liquid-liquid distribution coefficient[3134] countercurrent distribution,[2856] polarographic reduction,[3035] conformation in solution.[3097] Ionization constants: p$K_a$ 6.36, 9.90 (potentiometric, 25 °C),[353] 9.65 (UV, 20 °C),[3138] <2.3, 6.4, 10.1, >13.4 (NMR, 23 °C).[3083] Spectra: UV (fig.),[3043] far UV,[365] Raman (fig.),[3237] UV Raman (fig.),[3143] ORD (fig.),[3042] CD (fig.),[3043] [$^1$H] NMR (fig.),[3097] [$^{13}$C] NMR (fig.),[2946] [$^{31}$P] NMR,[68] 2d-[$^{13}$C-$^{31}$P] NMR,[2882] ESR (fig.),[2871] triplet-triplet absorption,[3238] ultrasound.[3047] Mass Spectra: EI-MS,[3145] FAB-MS,[3146] ESI-MS,[3147] PD-MS,[3148] EH-MS,[2888] SI-MS,[3204] CID-MS.[3149] Chromatography: PC,[3150] TLC,[3049] HPTLC,[3151] IEC,[3211] HPLC (ion exchange,[3152] ion pairing,[3153] ion suppression,[3154] reversed phase [3155]), GC,[2892] GC-MS,[3214] GFC,[2930] CC (activated carbon),[2896] MEKC.[3158] Electrophoresis: PE,[3159] TLE,[3161] CZE,[3163] CE,[2899] isotachophoresis.[3239] Theoretical calculations: extended Hückel,[3216] Hartree-Fock,[3166] thermodynamics,[3141] conformational energy.[3118]
$CaC_{10}H_{13}N_2O_8P{\cdot}2H_2O$ [R.N. 105280-62-4]: Monoclinic crystals, $d_c$ 1.697, X-ray structure[3240]; Raman,[3172] HF-CO.[3166] *Hexahydrate* [R.N. 175884-31-8]: Thin monoclinic plates, $d_m$ 1.58-1.61, X-ray structure[3241]; polarized crystal absorption spectrum (fig.).[3242]
$BaC_{10}H_{13}N_2O_8P$: Long, thin prisms (fig.), $[\alpha]_D^{21}$ − 4.4°($H_2O$),[3171] IR.[3079]
$(C_{23}H_{26}O_4N_2)_2C_{10}H_{15}N_2O_8P{\cdot}7H_2O$ (dibrucine salt): Needles, soften at 140 °C, mp ~175 °C.[3243]

Thymidine 5′-Diphosphate (TDP), $C_{10}H_{16}N_2O_{11}P_2$. *Thymidine 5′-(Trihydrogen Diphosphate)*

TDP [491-97-4]: Countercurrent distribution.[2856] Spectra: $^1$H, $^{13}$C, and $^{31}$P NMR.[2981] Chromatography: PC,[3025] IEC,[2894] HPLC (anion exchange,[2435] reversed phase,[3176] ion pairing [3177]), GFC.[2930] Electrophoresis: PE,[3244] CE,[3163] CZE,[2900] capillary isotachophoresis.[3239]
Ammonium salt (lyophilized): White powder.[2981]
$Ba_2(C_{10}H_{13}N_2O_{11}P)_2{\cdot}6H_2O$: White powder[3244]; IR.[3079]

Thymidine 5′-Triphosphate (TTP), $C_{10}H_{17}N_2O_{14}P_3$. *Thymidine 5′-(Tetrahydrogen Triphosphate)*

TTP [R.N. 365-08-2]: Countercurrent distribution.[2856] Spectra: UV,[3180] Raman,[3181] [$^1$H] and [$^{31}$P] NMR,[3180] FAB-MS,[3184] MALDI-MS,[3184] PD-MS.[3185] Chromatography: PC,[3025] TLC,[3049] IEC,[2894] HPLC (anion exchange,[2435] reversed phase,[3176] ion pairing[3177]), GFC,[2930] CC.[3180] Electrophoresis: PE,[3244] CE,[3163] CZE,[3186] capillary isotachophoresis.[3239]
$Na_4C_{10}H_{13}N_2O_{14}P_3{\cdot}2H_2O$: White nonhygroscopic water-soluble powder.[3096]
$Ba_2C_{10}H_{13}N_2O_{14}P_3{\cdot}5H_2O$. White solid.[3244]

## Synthesis

TMP may be prepared (a) by phosphorylation 3′-acetylthymidine with dibenzyl phosphorochloridate[3243] or 2-cyanoethyl phosphate[3066] or of 3′-DMT-thymidine with phosphoryl tris(triazolide),[3188] (b) by phosphorylation of unprotected thymidine with dibenzyl phosphorochloridate,[3245] di(2-*t*-butylphenyl)phosphorochloridate,[2977] diethylazodicarboxylate and triphenylphosphine,[3246] or $(CCl_3CMe_2O)_2P(O)Cl$,[3247] (c) by oxidation of thymidine 5′-phosphite with 2,2′-dipyridyl disulfide,[3248] (d) by hydrolysis of thymidine 5′-phosphorodiamidate,[3235] or (e) by fusion of 2,3-di-*O*-benzoyl-5-diphenylphosphoryl-D-ribofuranosyl bromide with trimethylsilylthymine.[3088]

TDP may be prepared (a) by the reaction of 5′-*O*-tosylthymidine with tris(tetra-*n*-butylammonium)pyrophosphate,[2981] (b) by successive reactions of 3′-*O*-benzylthymidine with phosphorylating agents containing protective substituents,[3244] (c) by phosphorylation of TMP with dibenzyl phosphorochloridate[2986] or ATP,[3192] or (d) by condensation of a TMP ester,[3012] thioester,[3249,3250] anhydride,[2989,3178,3180] or imidazolidate[3188] with tri-*n*-butylammonium phosphate.

TTP may be prepared (a) by successive reactions of 3′-*O*-acetylthymidine[3251] or 3′-*O*-benzylthymidine[3244] with phosphorylating agents containing protective substituents, (b) by condensation of a TMP ester,[3012] thioester,[3249] anhydride,[2989] imidazolidate,[3180,3193] or morpholidate[3096] with bis(tri-*n*-butylammonium)pyrophosphate, or (c) by enzymatic phosphorylation of TDP with ATP.[3192]

## Hydrolysis

TMP is resistant to hydrolysis under neutral or basic conditions but is hydrolyzed upon heating in acid, giving thymine and 2-deoxyribose-5-phosphate.[3196] A plot of log rate vs. $H_O$ at 75 °C is linear with slope −0.66 ($\Delta H$, $\Delta S$ given).[3224] In contrast, hydrolysis of TMP under neutral (pH 7.2, 50 °C) conditions in the presence of $CeCl_3$ catalyst cleaves the phosphate ester bond, giving thymidine. The rate constant $k$ is $4.5 \times 0^{-2}$ min$^{-1}$.[3199]

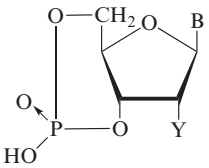
The hydrolysis of TTP over the pH range 2-10 parallels that of the ribonucleotides ATP, GTP, CTP, and UTP; the first-order rate constants are identical within experimental error. Its behavior toward Cu(II) and other metal ion catalysts is identical to that of UTP.[3128]

### Phosphorylation

Methods for the phosphorylation of TMP to TDP or TTP are described under the section "Synthesis" above. TMP is unaffected by sodium trimetaphosphate.[3029] The phosphorylation of thymidine with sodium dihydrogen phosphate under possibly primordial conditions (2 h at 160 °C) produces 6.3% of a mixture of 3′- and 5′-TMP [3252] (see also Ref. [3253]). The same reaction carried out under abiogenic conditions (1-9 h in vacuum UV) produces a 4.59% mixture of 3′- and 5′-TMP.[3254]

## Cyclic Ribonucleotides

Each of the foregoing ribo- and deoxyribonucleotides is capable of forming a cyclic monophosphate in which the phosphate group is linked to the 3′ and 5′ positions of the ribose ring, as illustrated:




B = A, G, C, U, or T
Y = H (T) or OH (others)

### Occurrence

Reports of the occurrence of cAMP in barley[3255] and lettuce[3256] in 1970 and others that followed were met with considerable skepticism. The levels were thought to be too low to play a significant role in plant metabolism and the methodology was inadequate. Several new methods that were specific for cAMP had to be developed before the existence of cAMP in higher plants was accepted; these methods are described in detail below. cGMP was identified in tobacco in 1973[2816] and all five of the cyclic nucleotides shown above were proven to be present in peas in 1989,[2829] though not in all tissues at the same time.

The metabolic pathway for the biosynthesis and degradation of cAMP is shown in Fig. 5-3. The pathways for the other cyclic nucleotides are unknown.

### Extraction and Separation

The cyclic nucleotides are extracted from plant tissue in the same manner as noncyclic nucleotides, but because the levels are so low (much lower than in animal or microbial tissues) no simple method of separation is adequate. In the procedure developed by

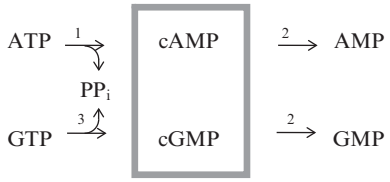



**FIGURE 5-3 Cyclic NMPs.** (1) Adenylate cyclase [E.C. 4.6.1.1], Mg(II) or Mn(II). (2) cNMP phosphodiesterase [E.C. 3.1.4.17], Mg(II). (3) Guanylate cyclase [E.C. 4.6.1.2], Mg(II), or Mn(II).

Brown and Newton,[2823] 6-day-old seedlings of *Phaseolus vulgaris* were extracted with methanol, chloroform, and 1*M* formic acid (12:5:3). The nucleotides were separated from other components by adsorption on charcoal and then separated from each other by IEC on Dowex 2-X8 ($Cl^-$), followed by IEC on Dowex 50-X4 ($H^+$), TLC on silica gel G, and finally high-voltage PE. The final product produced a single spot when cochromatographed with authentic cAMP by PC with five different eluants, TLC with three different eluants, and PE with three different buffers. The amounts determined by UV-visible spectrophotometry were between 2.6 and 9.2 nmol of cAMP per gram of seedling (dry wt.).[2823] In a later paper, Brown *et al.*[2824] confirmed these results by determining the cAMP level at each stage of the separation using the protein binding assay (PBA) described below, which is specific for cAMP. Most of the assay methods described on the following pages require prior purification of the cAMP (or cGMP), though not to the extent just described, in order to remove unknown substances that interfere with the assays. cCMP, cUMP, and cTMP have only been detected in plants by the FAB-MS/MS method; efforts to quantitate this method (as of this writing) have not been successful.[2829]

Pollard[3255] showed that 8-[$^{14}$C]-labeled adenine fed to germinating barley seeds produced a substance that appeared to be cAMP based on the usual criteria—chromatographic behavior, hydrolysis to 5′-AMP by phosphodiesterase, and deamination to cIMP—but similar experiments with other plants have been negative[2791] or inconclusive.[3257,3258]

## Special Methods for Cyclic Nucleotides

### *(1) Protein Binding Assay (PBA) Method*

The Gilman competitive protein binding assay, first applied to plant extracts independently by Bachofen,[2841] Becker and Ziegler,[2830] Brewin and Northcote,[2777] and Wellburn *et al.*[2780] in 1973, takes advantage of the specificity of cAMP-dependent protein kinase for cAMP. The method relies on the displacement of [$^3$H]-labeled cAMP from the protein by the cAMP in the extract. The following procedure is typical:

> *The reaction mixture in 200 μl of 0.05 M sodium acetate buffer, pH 4.0, contained: 3 pmoles $^3$H-cAMP (about 40000 cpm), varying concentration of unlabeled cAMP (ranging from 3 to 50 pmoles), or 50 μl of plant extract, respectively, and 20 μg of binding protein. The assay tubes were incubated in ice bath for 90 min. After that, the content of each reaction tube was diluted to 1 ml with 0.8 ml of cold 0.02 M potassium phosphate buffer, pH 6.0, and this mixture was filtered through a separate cellulose nitrate filter disc (pore size 0.45 μm). Then the filters were washed with 10 ml of cold buffer, dried, and placed in toluene scintillator, and finally counted in a liquid scintillation spectrometer.*
>
> Stroiński, A.; Floryszak-Wieczorek, J., "Adenosine 3':5'-Cyclic Monophosphate Changes during Germination of *Hordeum vulgare*", *Acta Physiol. Plant.* **1985**, *7*(2), 35–43,[2800] reprinted by permission of Elsevier, © 1985.

To avoid interference by substances that mimic the action of cAMP, it is essential that the cAMP, even after separation from other the other nucleotides, be further purified before assay by chromatography on alumina followed by Dowex 50.[2775,2781] Many

investigators have used the kits available from Boeringer Mannheim, Amersham, and other suppliers for this assay. cGMP may be assayed in the same manner using $^{3}$H-cGMP and a cGMP binding protein from silkworm pupae.[2827]

*(2) Protein Kinase Activation (PKA) Method*

This assay was first applied to plant extracts in 1973 by Raymond *et al.*,[2774] based on a procedure developed 3 years earlier by Kuo and Greengard. The amount of cAMP in the extract is determined by the amount of $^{32}$P transferred by the kinase from [$\gamma$-$^{32}$P]ATP to the substrate (histone).[2778] The following procedure is typical:

> *Under our standard assay conditions, each tube contained 0.05 M sodium acetate buffer (pH 6), 2 $\mu$mol magnesium acetate, 40 $\mu$g histone mixture, cAMP or plant extract in 100 $\mu$l, and 25 $\mu$l of cAMP-dependent protein kinase [from rabbit skeletal muscle]. Tubes were kept in ice during the addition of the enzyme. The reaction was commenced by the addition of 1000 pmol $\gamma$-$^{32}$P-ATP and tubes were incubated for 5 min at 30 C. The reactions were terminated by adding 2 ml of ice-cold trichloroacetic acid-tungstate-sulfuric acid mixture and processed [Kuo and Greengard, 1972]. The protein was finally collected by centrifugation, dissolved in 0.1 ml of 1 N NaOH, and suspended in 10 ml of Bray's scintillation fluid for counting. A standard curve with authentic cAMP was prepared for each experiment. . . .*
>
> Handa, A. K.; Johri, M. M., "Cyclic Adenosine 3':5'-Monophosphate in Moss Protonema", *Plant Physiol.* **1977**, *59*(3), 490–496,[2793] reprinted by permission of the American Society of Plant Biologists, © 1977.

This method is much more specific for cAMP than the protein binding method, but it too requires prior purification of the crude plant extract because of the presence of protein inhibitors.[2781] To avoid the need for $^{32}$P-labeled ATP, Handa and Bressan[2817] developed a modified protein kinase activation assay for use with plant extracts in which the consumption of ATP is measured instead by the firefly luminescence method.

*(3) Radioimmunoassay (RIA) Method*

This method, developed by Steiner in 1969, utilizes antisera that are specific for cAMP or cGMP. Like the protein binding method, it is based on competitive ligand binding between labeled and unlabeled cyclic nucleotide but is less subject to interference.[2429] The method was first applied to plant extracts independently by Lundeen *et al.*[2816] and Mascarenhas and Salomon[2779] in 1973. The following procedure is typical:

> *The dry residue after [chromatography on neutral alumina and] freeze-drying was taken up in 1 M perchloric acid; 0.1 mL of a 9 M KOH and 0.25 M EDTA solution was added to 0.5 mL of the perchloric extract; EDTA is needed to chelate $Mg^{2+}$. The precipitate (mainly $KClO_4$) was pelleted, and 0.15 mL of the supernatant was added to 6.75 mg of succinic anhydride. The succinylated sample was diluted six-fold*

*with $H_2O$. Final pH was between 5 and 6. Radioactive tracer (2'-O-succinyl cAMP [$^{125}$I]iodotyrosine methyl ester in 0.1 M citrate buffer, pH 6.2) was added, and the mixture was dialyzed against anti-cAMP antibodies dissolved in the same buffer. The standard curve and determinations were performed as in [T.T. Volker et al.[3259]].*

Spiteri, A.; Viratelle, O. M.; Raymond, P.; Rancillac, M.; Labouesse, J.; Pradet, A., "Artefactual Origins of Cyclic AMP in Higher Plant Tissues", *Plant Physiol.* **1989**, *91*(2), 624–628,[2795] reprinted by permission of the American Society of Plant Biologists, © 1989.

The analysis of cGMP requires an antiserum specific for cGMP. Many investigators have used the kits available from Amersham (UK), Yamasa (Japan), or Boehringer Mannheim (FRG) for this assay.

*(4) Mass Spectrometry (MS) Methods*

In 1980 Newton *et al.*[2820] provided the first mass spectrometric evidence confirming the existence of cAMP in a higher plant tissue, *P. vulgaris* leaf. The EI-MS spectrum of the trimethylsilylated cAMP exhibited ion fragments of the five- and six-membered rings that could only be derived from 3′:5′-cAMP and not from 2′:3′-cAMP nor any deoxy derivative. Janistyn[2838,2839] and Johnson *et al.*[2788] used GC-MS of the trimethylsilylated derivatives to quantify the content of cAMP[2788,2839] and cGMP[2838] in various plant tissues.

Using FAB-MS in combination with MIKES analysis of some of the resulting ions by collision-induced dissociation (CID), Newton *et al.*[2829] were able to identify all five of the common cyclic 3′,5′ nucleotides (cAMP, cGMP, cCMP, cUMP, and cTMP) as well as cIMP in purified but underivatized extracts of pea root. A closer examination of the cGMP extracted from bean leaf showed none of the 2′,3′ isomer.[2821] Witters *et al.*[2814] developed a procedure for measuring levels of these compounds in the $10^{-6}$ to $5 \times 10^{-9}$ M range in plant extracts by means of negative electrospray tandem MS in combination with ion suppression HPLC. Miniaturization of the HPLC setup by the use of capillary HPLC columns and precolumn switching lowered the detection limit to 25 fmol, enabling the analysis to be performed on mg amounts of plant tissue.[2815]

## Physical Properties

### Cyclic Adenosine 3′,5′-Phosphate (cAMP), $C_{10}H_{12}N_5O_6P$. *Adenosine, Cyclic 3′,5′-(Hydrogen Phosphate)*

cAMP [R.N. 60-92-4]: Fine orthorhombic needles, anhydrous, $d_m$ 1.75 (X-ray structure),[3260] DSC (fig.),[3261] countercurrent distribution[2776]; solubility in water 0.0236*M*, diffusion coefficient $4.44 \times 10^{-6}$ cm$^2$/s, $E_{max}$ $1.38 \times 10^{-4}$ (all at pH 7.0 and 20 °C)[3262]; polarographic reduction.[3135] Ionization constants: p$K_a$ 9.364 (potentiometric, 25 °C),[3263] ~13 (thermometric, 25 °C),[354] 3.6 ($^1$H NMR, 32 °C),[2863] 3.62 (electrophoretic, 20-25 °C).[3264] Spectra: UV,[3265] IR (fig.),[3266] Raman (fig.),[3142] UV Raman,[3267] ORD (fig.),[3268] CD (fig.),[3269] [$^1$H] NMR (fig.),[3270] [$^1$H] FT-NMR (fig.),[3271] [$^{13}$C] NMR (fig.),[3130] 2d-[$^{13}$C-$^1$H] NMR,[3272] [$^{31}$P] NMR[68]; EI-MS (TMS derivative),[2883] FAB-MS,[2911] FD-MS,[3095,3273] CIMS (fig.),[3274] ES-MS,[3275] LM-MS,[2889] thermospray MS,[3117]

MIKES (fig.),[2829] FAB-MS/MS,[2821] ES-MS/MS.[2814] Chromatography: PC,[3265] TLC, [3276] HPTLC,[3277] HPLC,[2825] GFC,[3278] GC-MS,[2838] alumina CC,[3279] Amberlite-XAD CC.[3280] Electrophoresis: PE,[3281] isotachophoresis,[3239] CZE,[3106] MEKC.[2901] Theoretical calculations: *ab initio* SCF,[3282] EHT,[3283,3284] PCILO.[3272] *cAMP·$H_2O$*: Crystalline solid.[3265] *cAMP·1.75$H_2O$*: Platelets with a pearly lustre, mp 219-220 °C dec. (corr.).[3266] Specific volume 0.60 at 24 °C; MW (ultracentrifugation) 320 (calc. 329).[2853]
$NaC_{10}H_{11}N_5O_6P$ [R.N. 33116-15-3]: DSC (fig.).[3261] *Tetrahydrate*: Monoclinic crystals, $d_c$ 1.558 (X-ray).[3285]

Cyclic Guanosine 3′,5′-Phosphate (cGMP), $C_{10}H_{12}N_5O_7P$. *Guanosine, Cyclic 3′,5′-(Hydrogen Phosphate)*

cGMP [R.N. 7665-99-8]: Orthorhombic crystals (X-ray structure),[3286] chemiluminescence,[3034] liquid crystals.[3038] Ionization constants: p$K_a$ −6.3 ($NH_3^+$), 18.6 ($NH_2$) ($^1$H NMR, 0 °C).[3287] Spectra: UV,[3265] IR,[3288] FT Raman (fig.),[3289] UV Raman,[3267] CD (fig.),[3290] [$^1$H] NMR (fig.),[3291] [$^{13}$C] NMR,[3130] [$^{31}$P] NMR,[3292] FAB-MS,[2821] MIKES,[2829] ES-MS/MS.[2814] Chromatography: PC,[3265] TLC,[2787] HPLC,[2825] GFC,[3293] GC-MS,[2838] alumina CC,[3279] Amberlite-XAD CC.[3280] Electrophoresis: PE,[3294] isotachophoresis,[3239] CZE.[3106]
$NaC_{10}H_{11}N_5O_7P$ [R.N. 40732-48-7]: DSC (fig.),[3261] Raman (fig.),[3041] FT Raman (fig.),[3289] ESR (fig.),[3295] ENDOR (fig.).[3295] *Tetrahydrate* [R.N. 52922-48-2]: Orthorhombic crystals, $d_m$ 1.66, $d_c$ 1.665 (X-ray structure).[3296]

Cyclic Cytidine 3′,5′-Phosphate (cCMP), $C_9H_{12}N_3O_7P$. *Cytidine, Cyclic 3′,5′-(Hydrogen Phosphate)*

cCMP [R.N. 3616-08-8]: Crystalline solid; DSC (fig.).[3261] Ionization constants: p$K_a$ 3.89 (potentiometric, 37 °C), ∼4.0 (UV, 37 °C).[3297] Spectra: UV,[3265] IR (fig.),[3298] [$^1$H] NMR (fig.),[3291] [$^{13}$C] NMR,[3130] CD (fig.),[3299] EI-MS,[2821] FAB-MS,[2821] FD-MS,[3273] MIKES,[2829] ES-MS/MS.[2814] Chromatography: PC,[3265] TLC,[3300] HPTLC,[3277] HPLC,[3301] GC (3,*N*-etheno, TMS derivative),[3087] alumina CC,[3279] Amberlite-XAD CC.[3280] Electrophoresis: PE,[3294] gel. [3298] *cCMP·3$H_2O$*: Transparent hexagonal platelike crystals, $d_c$ 1.40, $d_m$ 1.42 (X-ray structure).[3302]
$NaC_9H_{11}N_3O_7P·4H_2O$: Raman (fig.).[3041]

Cyclic Uridine 3′,5′-Phosphate (cUMP), $C_9H_{11}N_2O_6P$. *Uridine, Cyclic 3′,5′-(Hydrogen Phosphate)*

cUMP [R.N. 4004-57-3]: Transparent colorless monoclinic crystals, $d_m$ 1.530, $d_c$ 1.375 (X-ray structure),[3303] p$K_a$ 8.524 (potentiometric, 37 °C).[3297] Spectra: UV,[3265] CD (fig.),[3304] [$^1$H] NMR (fig.),[3305] [$^{13}$C] NMR,[3130] [$^{31}$P] NMR,[3144] FD-MS,[3273] MIKES.[2829] Chromatography: PC,[3265] TLC,[3300] HPTLC,[3277] HPLC,[3301] GFC,[3293] alumina CC,[3279] Amberlite-XAD CC.[3280] Electrophoresis: PE,[3294] CZE.[3106]
$NaC_9H_{10}N_2O_6P·4H_2O$ [R.N. 41092-63-1]: DSC (fig.).[3261]
$Et_3N·C_9H_{11}N_2O_6P$ [R.N. 20212-92-4]: Colorless crystalline solid, mp 220-223 °C dec.[3306]; tabular monoclinic plates, $d_m$ 1.38, $d_c$1.38 (X-ray structure).[3307]

Cyclic Thymidine 3′,5′-Phosphate (cTMP), $C_{10}H_{13}N_2O_7P$. *Thymidine, Cyclic 3′,5′-(Hydrogen Phosphate)*

cTMP [R.N. 6453-60-7]: Spectra: UV,[3308] IR,[3288] $^1$H NMR (fig.),[3309] $^{13}$C NMR,[3130] $^{31}$P NMR,[3144] MIKES.[2829] Chromatography: PC,[3308] TLC,[3310] HPTLC,[3277] HPLC.[3311] Electrophoresis: PE.[3308]

$NH_3 \cdot C_{10}H_{13}N_2O_7P$ [R.N. 119999-00-7]: White solid. Spectra: $^1$H NMR, $^{31}$P NMR.[3312]

## Conformation

Crystal X-ray analysis of cAMP shows that the asymmetric unit cell contains two molecules of cAMP which differ in their orientation about the glycosidic bond, one having a torsional angle of +102° and the other a torsional angle of −50°.[3260] In aqueous solution, according to $^1$H NMR analysis, the fused ribose and phosphate rings provide a rigid framework with the five-membered rings in the $^3$E conformation (3′-endo, 4′-exo) and the six-membered phosphate ring in the chair conformation.[3291,3309] The conformation of the adenine ring relative to the ribose phosphate framework, however, remains unresolved despite numerous efforts to determine its *syn-anti* distribution by ORD,[3268] ultrasonic relaxation,[3313] proton NMR lanthanide complexing,[3271,3314] [$^{13}$C] NMR analysis,[3130] potential energy[3315] or PCILO[3272] calculations, or supermolecular modeling.[3316] The most recent NMR studies suggest a 1:1 ratio of *syn* to *anti* at pH 2.0[3317] or 8.0,[3313] similar to that of the crystalline solid. In any event, the energy difference between the two conformers is only 1 kcal/mol[3283] and the barrier to rotation 6.6 kcal/mol.[3284]

Single-crystal X-ray analysis of cGMP, either as the acid[3286] or the sodium salt,[3296] shows that it has but one molecule per unit cell in which the base displays the *syn* conformation with a glycosyl torsional angle of −102°.[3296] In aqueous solution, according to $^1$H NMR analysis, the conformation is similar to that of cAMP with respect to the ribose and phosphate rings,[3291] but is predominantly *syn* about the glycosyl bond owing to hydrogen bonding between the guanine $NH_2$ and the axial ribose OH. This conformation is supported by AMI,[3318] Hartree-Fock,[3318] PCILO,[3272] potential energy,[3315] and EHMO[3319] calculations.

The conformation of cCMP in aqueous solution[3268] is similar to that of cAMP, but the ribose ring of cCMP.3$H_2O$ in the solid state is 3′-endo, 2′-exo,[3302] unlike any of the other cyclic NMPs. Theoretical calculations by the potential energy[3315] or PCILO[3272] methods suggest that the conformation about the glycosidic linkage is predominantly *anti*.

Single-crystal X-ray analysis of cUMP shows that it has an asymmetric unit cell that contains two molecules, one having a torsional angle of −77° and the other of −58° between the base and the ribose.[3307] In aqueous solution, the conformation is similar to that of cAMP with respect to the ribose and phosphate rings[3291] but probably *anti* with respect to the glycosyl bond.[3320] The conformation is *anti* in both molecules in the crystal,[3307] and theoretical calculations based on EHMO,[3319] PCILO,[3272] or potential energy[3315] methods suggest that it is predominantly *anti* in solution.

The conformation of cTMP in aqueous solution, based on $^1$H NMR analysis, is similar to that of cAMP with the five-membered deoxyribose ring in the $^3$E conformation (4′-exo) and the six-membered phosphate ring in the chair conformation,[3309] but the ribose ring is

flatter owing to the absence of the 2′-OH group.[3291] The torsional angle around the glycosidic bond is in the *anti* range in the preferred conformation.[3321] There are no X-ray data available for cTMP so its conformation in the solid state is unknown.

## Synthesis

cAMP may be prepared (a) from adenosine by phosphorylation with $POCl_3$ in trimethyl phosphate followed by cyclization with aqueous KOH[3322]; (b) from AMP by cyclization with DCC[3265] or TPP/PDS[3323] in pyridine; (c) from a 5′-AMP *p*-nitrophenyl or 8-quinolyl ester by cyclization with acetic acid/pyridine,[3324] CuCl/pyridine,[3325] or *t*-BuOK/DMSO[3326]; (d) from a 5′-AMP thioester by cyclization with $I_2$/pyridine[3294]; (e) from 5′-AMP diphenylphosphinothioic anhydride by cyclization with $Bu_3N$/pyridine[2989]; (f) from a 2′-protected 3′-AMP diphenyl ester by cyclization with *t*-BuOK/DMSO[3327]; (g) from the *p*-trichloromethyl derivative of AMP by cyclization with *t*-BuOK/DMSO[3328]; or (h) from ATP by hydrolysis with aqueous $Ba(OH)_2$.[3266]

cGMP may be prepared from guanosine by method (a),[3322] from GMP or its *N*-benzoyl derivative by method (b),[3265,3323] from a 5′-GMP ester by method (c),[3324–3326] from a 5′-GMP thioester by method (d),[3294] or from the P-$CCl_3$ derivative of GMP by method (g).[3328]

cCMP may be prepared from CMP or its *N*-benzoyl derivative by method (b),[3265,3323] from a 5′-CMP ester by method (c),[3324–3326] from a 5′-CMP thioester by method (d),[3294] or from the P-$CCl_3$ derivative of CMP by method (g).[3328]

cUMP may be prepared from UMP by method (b),[3265,3323] from a 5'-UMP ester by method (c),[3324–3326] from a 5′-UMP thioester by method (d),[3294] from a 5-UMP anhydride by method (e),[2989] from a 2′-protected 3′-UMP diphenyl ester by method (f),[3327] or from the P-$CCl_3$ derivative of UMP by method (g).[3328]

cTMP may be prepared from TMP by method (b),[3308,3323] from a 3′- or 5′-TMP *p*-nitrophenyl, 8-quinolyl or diphenyl ester by method (c),[3324,3325,3327] from a 5′-TMP anhydride by method (e),[2989] or from the methyl ester of cTMP by refluxing with *t*-butylamine.[3312]

Phosphorylation of adenosine with phosphorus pentoxide under prebiotic conditions yields only traces of 3′,5′-cAMP. The principal products are 2′-AMP, 3′-AMP, and 2′,3′-cAMP.[3329]

## Hydrolysis

Hydrolysis of cAMP with 1*N* HCl at 100 °C yields adenine and $P_i$ with only trace amounts of ribose phosphates.[3265] The rate constant at 90 °C is $0.184 \times 10^{-3}\ s^{-1}$ compared to $2.5 \times 10^{-3}\ s^{-1}$ for AMP; the difference is ascribed to the rigidity of the fused ring which retards the formation of a planar cyclic oxocarbenium ion.[3330] Hydrolysis of cAMP with 0.2*M* $Ba(OH)_2$ for 30 min at 100 °C results in a 5:1 mixture of 3′-AMP and 5′-AMP with no trace of 2′-AMP.[3265] Under much milder conditions (pH 8, 37 °C), the hydrolysis of cAMP is catalyzed by $Co^{III}$ complexes such as $Co(trien)(H_2O)^{3+}$[3331] and by lanthanides[3332] or their germanium complexes.[3333] By far the most efficient lanthanides are $Ce^{III}$ and its cluster $[Ce_3(OH)_5]^{4+}$, which decrease the half-life of cAMP from 600,000 years to 1-2 min and 35 s, respectively, an effect attributed to the oxidation of the $Ce^{III}$ to $Ce^{IV}$ in air; the P–O(5′) bond is cleaved first.[3332]

The behavior of cGMP toward acid- or base-catalyzed hydrolysis parallels that of cAMP, its half-life in 1*N* HCl at 100 °C being 28 min vs. 30 min for cAMP, 26 min for cCMP, 8 min for cUMP,[3265] and 13 min (at 50 °C) for cTMP.[3334] Under much milder conditions (pH 7, 30 °C), the hydrolysis of cGMP is catalyzed by Ce(III)[3332] or its germanium complex[3333] and even more strongly by Ce(IV).[3332,3335]

The second-order rate constant for the hydrolysis of cCMP with 1*N* HCl at 90 °C is $0.200 \times 10^{-3}$ s$^{-1}$, the product being a mixture of 2′-, 3′-, and 5′-CMP owing to rapid phosphate migration. Under less acidic conditions (pH > 2) cleavage of the *N*-glycosidic bond predominates, liberating cytidine.[3330] Hydrolysis of cCMP with 0.2*M* $Ba(OH)_2$ at 100 °C results in a 5:1 mixture of 3′- and 5′-monophosphates but the reaction is complicated by extensive deamination of cytidine to uracil.[3265]

The glycosyl bond in cUMP is strikingly acid-labile; the hydrolysis evidently proceeds by a different mechanism, involving opening of the ribose ring via a Schiff base intermediate in contrast to the cyclic oxycarbenium ion mechanism proposed for the other cNMPs. The rate constants for the hydrolysis of cUMP with 1*N* HCl at 90 °C are $0.251 \times 10^{-3}$ s$^{-1}$ for the glycosyl bond and $0.272 \times 10^{-3}$ s$^{-1}$ for the competing hydrolysis of the phosphate group to 5′-UMP and 3′(2′)-UMP.[3330]

The first-order rate constant for the hydrolysis of cTMP in 1*N* HCl at 90 °C is $4.07 \times 10^{-3}$ s$^{-1}$ compared to $0.0053 \times 10^{-3}$ s$^{-1}$ for TMP.[3330] The only chromophoric product is thymine.[3334] Hydrolysis of cTMP with 1*N* NaOH at 100 °C ($t_{1/2}$ 2 h) yields a 5:1 mixture of 3′-TMP and 5′-TMP.[3308] Under much milder conditions (pH 8.0, 30 °C) the pseudo-first-order rate constant for the hydrolysis of cTMP by Ce(IV) is 1.2 min$^{-1}$.[3335]

## Energetics of Hydrolysis

In a study of the adenylate cyclase reaction, the standard free energy of hydrolysis ($\Delta G^\circ$) of cAMP to 5′-AMP at pH 7.3 was found to be −11.9 kcal/mol, compared to −8.9 kcal/mol for the hydrolysis of ATP to ADP and $P_i$.[3336] This value is unexpectedly high and places cAMP in a class with "energy-rich" phosphates like PEP or creatine phosphate. Several studies were undertaken in the 1970s to explain this phenomenon.

The free energy of a reaction ($\Delta G$) comprises an enthalpy component ($\Delta H$) and an entropy component ($\Delta S$). The enthalpy of hydrolysis of cAMP to 5′-AMP at pH 7.3 and 25 °C was found to be −14.1 kcal/mol in a microcalorimetric study of the phosphodiesterase reaction.[3337] In a later study this figure was revised to −11.1 kcal/mol.[3338] Nevertheless, these studies indicate that the large exergonic change that takes place during the hydrolysis of cAMP to AMP is associated primarily with a change in enthalpy rather than entropy. From the relation $\Delta G' = \Delta H + T\Delta S$, the value of $\Delta S'$ calculated from the data above is only −7.4 or +2.7 cal/deg/mol, respectively.

The enthalpy of hydrolysis of cAMP is about 8 kcal/mol more exothermic than that of trimethylene phosphate, a model compound with a similar six-membered phosphate ring.[3282] Theoretical calculations using molecular mechanics and *ab initio* methods suggest that about 4-5 kcal/mol arise from the *trans* ring fusion, which results in a puckering

of the ribose ring, and about 1-2 kcal/mol arise from an unfavorable O–C–C–O interaction which is relieved upon cleavage of the phosphate ring.[3282] The remaining 1-2 kcal/mol appear to arise from solvation of 5′-AMP (but not of cAMP) by water.[3339]

The enthalpy of hydrolysis of cGMP to 5′-GMP by bovine phosphodiesterase at 25 °C was found to be −10.5 kcal/mol,[3337] compared to −14.1 kcal/mol for cAMP and −12.0 kcal/mol for the hydrolysis of cUMP to 5′-UMP by canine phosphodiesterase at 25 °C.[3340]

**Table 5-4** Cyclic Ribonucleotides in Plants

| No. | Plant part | Method | cAMP | cGMP | cCMP | cUMP | cTMP | References |
|---|---|---|---|---|---|---|---|---|
| *Acer pseudoplatanus* L. (Sycamore Maple) | | | | | | | | |
| 1 | Seed embryo and axis | PBA | 0.018 | | | | | 2773 |
| 1 | –, embryo, and axis | RIA | | 0.083 | | | | 2773 |
| 1 | –, cotyledon | PBA | 0.007 | | | | | 2773 |
| 1 | –, cotyledon | RIA | | 0.009 | | | | 2773 |
| 1 | Cell suspension culture | FFL | 0.140 | | | | | 2774 |
| 1 | Cell suspension culture | PKA | 0.123 | | | | | 2774 |
| *Agave americana* ssp. *marginata* Trel (Maguey) | | | | | | | | |
| 1 | Leaf | PBA | 0.001 | | | | | 2775 |
| 1 | Leaf | PKA | 0.0009 | | | | | 2775 |
| *Apium graveolens* L. (Celery) | | | | | | | | |
| 1 | Leaf | PBA | <0.0028 | | | | | 2776 |
| *Avena sativa* L. (Oats) | | | | | | | | |
| 1 | Coleoptile | PBA | 0.120 | | | | | 2777 |
| 1 | Coleoptile | PKA | <0.0025 | | | | | 2778 |
| 1 | Coleoptile | RIA | 0.520 | | | | | 2779 |
| 1 | Etioplast[a] | PBA | 0.067 | | | | | 2780 |
| 1 | Seedling, leaf, and coleoptile | PBA | 0.0464 | | | | | 2781 |
| 1 | Seedling, leaf, and coleoptile | PKA | 0.0019 | | | | | 2781 |
| *Brassica chinensis* L. (Chinese Cabbage) | | | | | | | | |
| 1 | Leaf | FFL | 0.890 | | | | | 2774 |
| *Brassica oleracea* L. ssp. *capitata* L. (Cabbage) | | | | | | | | |
| 1 | Leaf | FFL | 2.00 | | | | | 2782 |
| *Campanula* spp. (Chinese Bellflower) | | | | | | | | |
| 1 | Root | PBA | 0.00288 | | | | | 2783 |
| *Catharanthus roseus* (L.) G. Don (Madagascar Periwinkle) | | | | | | | | |
| 1 | Cell tissue culture | PKA | <0.0005 | | | | | 2778 |
| 1 | Callus culture[b] | RIA | 0.143 | | | | | 2784 |

**Table 5-4** Cyclic Ribonucleotides in Plants—cont'd

| No. | Plant part | Method | cAMP | cGMP | cCMP | cUMP | cTMP | References |
|---|---|---|---|---|---|---|---|---|
| *Ceratophyllum demersum* L. (Hornwort) | | | | | | | | |
| 1 | Whole plant | FFL | 0.030 | | | | | 2785 |
| 1 | Whole plant | PBA | 0.026 | | | | | 2785 |
| *Cicer arietinum* L. (Chickpea) | | | | | | | | |
| 1 | Seed | $^{14}$C-adenine | 0.036 | | | | | 2786 |
| *Citrus limettiodes* Tanaka (Sweet Lime) | | | | | | | | |
| 1 | Leaf | PBA | 0.230 | | | | | 2787 |
| *Citrus limon* L. (Lemon) | | | | | | | | |
| 1 | Young leaf | GC-MS | 0 | | | | | 2788 |
| 1 | Young leaf | RIA | 0.028 | | | | | 2788 |
| *Citrus sinensis* (L.) Osbeck Shamouti Orange | | | | | | | | |
| 1 | 7-day growth flush | PBA | 0.380 | | | | | 2787 |
| *Citrus unshiu* Marc. (Mandarin) | | | | | | | | |
| 1 | Leaf | PBA | 0.340 | | | | | 2787 |
| 1 | Root | PBA | 0.350 | | | | | 2787 |
| *Cocos nucifera* L. (Coconut) | | | | | | | | |
| 1 | Nut, endosperm | RIA | 4.4-4.6 | | | | | 2789 |
| *Coleus blumei* Benth. (Painted Nettle) | | | | | | | | |
| 1 | Leaf | PBA | <0.0015 | | | | | 2776 |
| 1 | Stem | PBA | <0.0037 | | | | | 2776 |
| *Cucumis sativus* L. (Cucumber) | | | | | | | | |
| 1 | Leaf | PBA | <0.0061 | | | | | 2776 |
| 1 | Stem | PBA | <0.0080 | | | | | 2776 |
| 1 | Seedling, cotyledon | PBA | 0.252 | | | | | 2787 |
| 1 | Root | PBA | 0.0533 | | | | | 2776 |
| 1 | Root | PBA | 0.216 | | | | | 2787 |
| *Datura* spp. (Thorn Apple) | | | | | | | | |
| 1 | Leaf | PBA | 0.132 | | | | | 2787 |
| *Daucus carota* L. (Carrot) | | | | | | | | |
| 1 | Root | PBA | 0.00114 | | | | | 2783 |
| 1 | Pith tissue culture | FFL | 0.153 | | | | | 2774 |
| 1 | Pith tissue culture | PKA | 0.134 | | | | | 2774 |
| 1 | Cell culture[b] | RIA | 0.050 | | | | | 2790 |
| *Dicranella coarctata* (C. Müll) Bosch and Sande Lac. | | | | | | | | |
| 1 | Protonemal tissue | $^{14}$C-Adenine | <0.001 | | | | | 2791 |
| *Evodia officinalis* Dode | | | | | | | | |
| 1 | Fruit[c] | RIA | | 36.8 | | | | 2792 |
| 1 | –, peduncle[c] | RIA | | 11.0 | | | | 2792 |
| *Evodia rutaecarpa* (Juss.) Benth. | | | | | | | | |
| 1 | Fruit[c] | RIA | | 31.2 | | | | 2792 |
| 1 | –, peduncle[c] | RIA | | 27.0 | | | | 2792 |

[a]nmol/mg protein. [b]nmol/L. [c]Dry weight basis. [d]nmol/$10^6$ protoplasts. [e]nmol/mg chlorophyll.

*Continued*

**Table 5-4** Cyclic Ribonucleotides in Plants—cont'd

| No. | Plant part | Method | cAMP | cGMP | cCMP | cUMP | cTMP | References |
|---|---|---|---|---|---|---|---|---|
| *Fumaria hygrometrica* (L.) Sibth | | | | | | | | |
| 1 | Cell suspension culture | PBA | 0.063 | | | | | 2793 |
| 1 | Cell suspension culture | PKA | 0.0315 | | | | | 2793 |
| 1 | Protonemal filaments | $^{14}$C-Adenine | <0.001 | | | | | 2791 |
| 1 | Gametophyte tissue | $^{14}$C-Adenine | <0.001 | | | | | 2791 |
| *Glycine max* (L.) Merr. (Soybean) | | | | | | | | |
| 1 | Seed, hypocotyl | RIA | 0.0006 | | | | | 2794 |
| 1 | Cell suspension culture | RIA | 0 | | | | | 2794 |
| 1 | Callus culture | PBA | 0.027 | | | | | 2777 |
| *Helianthus annuus* L. (Sunflower) | | | | | | | | |
| 1 | Seed | RIA | <0.0005 | | | | | 2795 |
| 1 | Embryo | RIA | <0.0005 | | | | | 2795 |
| 1 | Seedling | RIA | <0.0005 | | | | | 2795 |
| 1 | Callus culture | PBA | 0.125 | | | | | 2796 |
| 1 | Callus culture | PKA | 0.0096 | | | | | 2796 |
| 1 | Callus culture[b] | RIA | 0.131 | | | | | 2784 |
| *Helianthus tuberosus* L. (Jerusalem Artichoke) | | | | | | | | |
| 1 | Tuber, dormant | RIA | 0.060 | | | | | 2797 |
| 1 | –, sprouting | RIA | 0.025 | | | | | 2797 |
| *Hordeum vulgare* L. (Barley) | | | | | | | | |
| 1 | Seed[c] | FFL | 0.420 | | | | | 2782 |
| 1 | Seed | PBA | n.d. | | | | | 2798 |
| 1 | Seed | PKA | n.d. | | | | | 2798 |
| 1 | Seed[c] | RIA | 0.2-2 | | | | | 2799 |
| 1 | Seed | PBA | 0.0002 | | | | | 2800 |
| 1 | Seed | RIA | | 0.000032 | | | | 2801 |
| 1 | –, embryo | PBA | 0.160 | | | | | 2787 |
| 1 | Seedling, coleoptile | PBA | 0.0037 | | | | | 2800 |
| 1 | –, coleoptile | RIA | | 0.000200 | | | | 2801 |
| 1 | –, root | PBA | 0.0112 | | | | | 2800 |
| 1 | –, root | RIA | | 0.000147 | | | | 2801 |
| *Impatiens sultanii* Hook. f. (Sultana) | | | | | | | | |
| 1 | Young leaf | PBA | 0.92 | | | | | 2802 |
| 1 | Old leaf | PBA | 0.22 | | | | | 2802 |
| *Kalanchoë daigremontiana* Ham. and Per. (Devil's Backbone) | | | | | | | | |
| 1 | Leaf | PBA | 0.006 | | | | | 2775 |
| 1 | Leaf | PKA | 0.005 | | | | | 2775 |

**Table 5-4** Cyclic Ribonucleotides in Plants—cont'd

| No. | Plant part | Method | cAMP | cGMP | cCMP | cUMP | cTMP | References |
|---|---|---|---|---|---|---|---|---|
| *Lactuca sativa* L. (Lettuce) | | | | | | | | |
| 1 | Seed | FFL | 0.241 | | | | | 2774 |
| 1 | Seed | PKA | 0.269 | | | | | 2774 |
| 1 | Seed | RIA | 0.0085 | | | | | 2795 |
| 1 | –, without external tegument | RIA | <0.0005 | | | | | 2795 |
| 1 | –, germinated | PBA | 0.022 | | | | | 2781 |
| 1 | –, germinated | PKA | 0.0026 | | | | | 2781 |
| 1 | Seedling leaf and root | PBA | 0.265 | | | | | 2787 |
| *Lemna gibba* L. (Duckweed) | | | | | | | | |
| 1 | Whole plant | PBA | 1.040 | | | | | 2787 |
| *Lemna paucicostata* Hegelm. (Lesser Duckweed) | | | | | | | | |
| 1 | Whole plant | HPLC | 0.075 | | | | | 2803 |
| 1 | 6-day plant[c] | RIA | 0.014 | | | | | 2804 |
| 1 | 10-day plant[c] | RIA | 0.023 | 0.17 | | | | 2805 |
| *Lilium longiflorum* Thunb. (Trumpet Lily) | | | | | | | | |
| 1 | Flower, anther | RIA | 0.0089 | | | | | 2806 |
| 1 | –, filament | RIA | 0.0009 | | | | | 2806 |
| 1 | –, ovary | RIA | 0.0059 | | | | | 2806 |
| 1 | –, upper style | RIA | 0.0151 | | | | | 2806 |
| 1 | –, lower style | RIA | 0.0043 | | | | | 2806 |
| 1 | –, tepal | RIA | 0.0008 | | | | | 2806 |
| *Lolium multiflorum* Lam. (Italian Ryegrass) | | | | | | | | |
| 1 | Endosperm cell suspension culture | PBA | 0.014 | | | | | 2807 |
| 1 | Endosperm cell suspension culture | PKA | 0.012 | | | | | 2807 |
| *Lupinus arboreus* Sims (Tree Lupine) | | | | | | | | |
| 1 | Root | PBA | <0.0012 | | | | | 2776 |
| 1 | –, nodule | PBA | 0.0412 | | | | | 2776 |
| *Lycopersicon esculentum* Mill. (Tomato) | | | | | | | | |
| 1 | Seedling | PKA | <0.0015 | | | | | 2778 |
| 1 | Cell suspension culture | PBA | 0.00164 | | | | | 2808 |
| *Mangifera indica* L. (Mango) | | | | | | | | |
| 1 | Young (apical) leaf | PBA | 4.80 | | | | | 2787 |
| 1 | Old (basal) leaf | PBA | 2.80 | | | | | 2787 |
| 1 | Root | PBA | 1.56 | | | | | 2787 |
| *Medicago sativa* L. (Alfalfa) | | | | | | | | |
| 1 | Callus suspension culture FAB-MS | | + | | | | | 2809 |
| 1 | Callus suspension culture FAB-MS | RIA | 0.0004 | | | | | 2809 |

[a]nmol/mg protein. [b]nmol/L. [c]Dry weight basis. [d]nmol/$10^6$ protoplasts. [e]nmol/mg chlorophyll.

*Continued*

**Table 5-4** Cyclic Ribonucleotides in Plants—cont'd

| No. | Plant part | Method | cAMP | cGMP | cCMP | cUMP | cTMP | References |
|---|---|---|---|---|---|---|---|---|
| *Najas flexilis* (Willd.) Rostk. and Schmidt (Water Nymph) | | | | | | | | |
| 1 | Whole plant | FFL | 0.050 | | | | | 2785 |
| 1 | Whole plant | PBA | 0.053 | | | | | 2785 |
| | | and diurnal variation | | | | | | 2810 |
| *Nicotiana glutinosa* L. (Tobacco) | | | | | | | | |
| 1 | Leaf | RIA | | 0.000343 | | | | |
| | 2811 | | | | | | | |
| *Nicotiana suaveolens* Lehm. × *N. langsdorffii* | | | | | | | | |
| 1 | Stem | RIA | 0.0236 | | | | | 2812 |
| *Nicotiana tabacum* L (Tobacco) | | | | | | | | |
| 1 | Leaf | HPLC | 0.0028 | | | | | 2813 |
| 1 | –, chloroplast | HPLC-MS | 0.0029 | | | | | 2814 |
| 1 | Seedling, leaf | PBA | 0.055 | | | | | 2787 |
| 1 | –, apical bud | PBA | 0.216 | | | | | 2787 |
| 1 | –, stem | PBA | 0.056 | | | | | 2787 |
| 1 | –, root | PBA | 0.070 | | | | | 2787 |
| 1 | Shoot, meristem apex | HPLC-MS | 0.0178 | | | | | 2815 |
| 1 | Cell tissue culture | PKA | <0.0005 | | | | | 2778 |
| 1 | Callus culture | PKA | 0.0061 | | | | | 2781 |
| 1 | Callus culture | GC-MS | 0.137 | | | | | 2788 |
| 1 | Callus culture | RIA | 0.378 | | | | | 2788 |
| 1 | Pith tissue culture | FFL | 0.095 | | | | | 2774 |
| 1 | Pith tissue culture | PKA | 0.084 | | | | | 2774 |
| 1 | Pith parenchyma | PKA | <0.0009 | | | | | 2778 |
| 1 | Pith parenchyma[c] | RIA | 0.40 | 0.050 | | | | 2816 |
| 1 | Axenic cell culture | PKA | | | | | | 2817 |
| | | 0.0005-0.003 | | | | | | |
| *Nuphar advena* Ait. (Spatterdock) | | | | | | | | |
| 1 | Whole plant | FFL | 0.026 | | | | | 2785 |
| 1 | Whole plant | PBA | 0.029 | | | | | 2785 |
| *Oryza sativa* L. (Rice) | | | | | | | | |
| 1 | Embryo | RIA | <0.0005 | | | | | 2795 |
| 2 | Shoot (1) | PBA | 0.0042 | | | | | 2818 |
| 1 | Shoot (2) | PBA | 0.0020 | | | | | 2818 |
| 1 | Seedling | RIA | <0.0005 | | | | | 2795 |
| *Panax ginseng* C. Meyer (Ginseng) | | | | | | | | |
| 1 | Root | PBA | 0.00113 | | | | | 2783 |
| *Persea americana* Mill. (Avocado) | | | | | | | | |
| 1 | Young (apical) leaf | PBA | 9.60 | | | | | 2787 |
| 1 | Old (basal) leaf | PBA | 4.90 | | | | | 2787 |
| 1 | White root | PBA | 1.30 | | | | | 2787 |
| *Petroselinum crispum* Mill. (Parsley) | | | | | | | | |
| 1 | Cell suspension culture | RIA | 0.006 | | | | | 2819 |
| 1 | Protoplast[d] | RIA | 0.003 | | | | | 2819 |

**Table 5-4** Cyclic Ribonucleotides in Plants—cont'd

| No. | Plant part | Method | cAMP | cGMP | cCMP | cUMP | cTMP | References |
|---|---|---|---|---|---|---|---|---|
| *Phaseolus vulgaris* L. (Beans) | | | | | | | | |
| 1 | Leaf | GC-MS | + | | | | | 2820 |
| 1 | Leaf | FAB-MS | | + | | | | 2821 |
| 1 | Leaf, protoplast[a] | PBA | 0.400 | | | | | 2822 |
| 1 | Seedling[c] | UV-Vis | 2.6-9.2 | | | | | 2823 |
| 1 | Seedling[c] | PBA | 2.2 | | | | | 2824 |
| 1 | Seedling[c] | PKA | 0.0136 | | | | | 2825 |
| 1 | Seedling[c] | HPLC | 0.0197 | | | | | 2825 |
| 1 | Shoot[c] | PBA | 0.0046 | | | | | 2826 |
| 1 | –, chloroplast[a] | PBA | 0.0383 | | | | | 2826 |
| 1 | –, chloroplast[a] | RIA | | 0.020 | | | | 2826 |
| 1 | Root, meristem | RIA | | 0.020 | | | | 2805 |
| | | and variation in concentration along the root | | | | | | 2805 |
| *Phaseolus vulgaris* L. ssp. *napus* (Dwarf Bean) | | | | | | | | |
| 1 | Seedling | GC-MS | 0.100 | | | | | 2788 |
| 1 | Seedling | RIA | 0.281 | | | | | 2788 |
| *Pinus densiflora* Sieb. and Zucc. (Japanese Red Pine) | | | | | | | | |
| 1 | Pollen | PBA | 0.23 | 0.06 | | | | 2827 |
| *Pinus pinaster* Ait. (Cluster Pine) | | | | | | | | |
| 1 | Embryo | RIA | <0.0005 | | | | | 2795 |
| 1 | Needle (leaf) | RIA | <0.0005 | | | | | 2795 |
| *Pinus radiata* D. Don (Monterey Pine) | | | | | | | | |
| 1 | Seed | PBA | 0.0168 | | | | | 2776 |
| 1 | Old needle (leaf) | PBA | 0.0384 | | | | | 2776 |
| 1 | Young needle | PBA | 0.0096 | | | | | 2776 |
| 1 | Spring shoot | PBA | <0.0017 | | | | | 2776 |
| 1 | Male flower | PBA | 0.0627 | | | | | 2776 |
| 1 | Female flower | PBA | <0.0024 | | | | | 2776 |
| *Pinus taeda* L. (Loblolly Pine) | | | | | | | | |
| 1 | Callus culture | PBA | 0.125 | | | | | 2828 |
| *Pisum sativum* L. (Pea) | | | | | | | | |
| 1 | Seed, embryo | PBA | 0.176 | | | | | 2787 |
| 1 | Leaf[a] | PBA | 0.179 | | | | | 2822 |
| 1 | Root tip | FAB-MS | + | + | + | + | 0 | 2829 |
| 1 | Nonmeristematic root segment | FAB-MS | + | + | + | + | + | 2829 |
| *Potamogeton zosteriformis* Fern. (Flatstem Pondweed) | | | | | | | | |
| 1 | Whole plant | FFL | 0.028 | | | | | 2785 |
| 1 | Whole plant | PBA | 0.025 | | | | | 2785 |
| *Raphanus sativus* L. (Radish) | | | | | | | | |
| 1 | Root | PBA | 0.00120 | | | | | 2783 |
| *Robinia pseudoacacia* L. (Black Locust) | | | | | | | | |
| 1 | Sieve-tube sap[b] | PBA | 9.0 | | | | | 2830 |

[a]nmol/mg protein. [b]nmol/L. [c]Dry weight basis. [d]nmol/$10^6$ protoplasts. [e]nmol/mg chlorophyll.

*Continued*

**Table 5-4** Cyclic Ribonucleotides in Plants—cont'd

| No. | Plant part | Method | cAMP | cGMP | cCMP | cUMP | cTMP | References |
|---|---|---|---|---|---|---|---|---|
| *Rubus* spp. (Bramble) | | | | | | | | |
| 1 | Pith tissue culture | FFL | 0.142 | | | | | 2774 |
| *Scirpus subterminalis* Torr. | | | | | | | | |
| 1 | Whole plant | FFL | 0.048 | | | | | 2785 |
| 1 | Whole plant | PBA | 0.053 | | | | | 2785 |
| | | and diurnal variation | | | | | | 2810 |
| *Secale cereale* L. (Rye) | | | | | | | | |
| 1 | Seedling | HPLC | 0.700 | | | | | 2831 |
| *Sinapis alba* L. (White Mustard) | | | | | | | | |
| 1 | Seedling | PBA | 0.114 | | | | | 2832 |
| *Solanum tuberosum* L (Potato) | | | | | | | | |
| 1 | Tuber | PBA | 0.028 | | | | | 2833 |
| 1 | Tuber | RIA | 30.2-40.1 | 14.0-15.2 | | | | 2834 |
| *Spirodela oligorrhiza* (Kurz.) Hegelm. (Duckweed) | | | | | | | | |
| 1 | Whole plant | PBA | 0.0110 | | | | | 2776 |
| *Trifolium repens* L. (White Clover) | | | | | | | | |
| 1 | Leaf[b] | PBA | 0.0132 | and diurnal variation | | | | 2835 |
| *Triticum aestivum* L. (Wheat) | | | | | | | | |
| 1 | Embryo (germ) | PBA | 0.0111 | | | | | 2776 |
| 1 | Leaf | PBA | 0.180 | | | | | 2787 |
| 1 | Root | PBA | 0.170 | | | | | 2787 |
| *Vicia faba* L. (Faba Bean) | | | | | | | | |
| 1 | Seedling | UV-Vis | 0 | | | | | 2823 |
| 1 | Internode | PBA | 0 | | | | | 2836 |
| *Vigna mungo* (L.) Hepper (Black Gram) | | | | | | | | |
| 1 | Seedling, shoot | PBA | 0.0174 | | | | | 2837 |
| 1 | –, root | PBA | 0.0085 | | | | | 2837 |
| *Zea mays* L. (Corn) | | | | | | | | |
| 1 | Kernel | GC-MS | 0.079 | | | | | 2788 |
| 1 | Kernel | RIA | 0.274 | | | | | 2788 |
| 1 | Seedling | GC-MS | | 0.072 | | | | 2838 |
| 1 | Seedling[c] | GC-MS | 6.808 | | | | | 2839 |
| 1 | Seedling | PBA | 0.035 | | | | | 2840 |
| 1 | –, chloroplast[e] | PBA | 0.594 | | | | | 2840 |
| 1 | –, coleoptile tip[c] | PBA | 1.3 | | | | | 2841 |
| 1 | –, shoot[c] | HPLC | 0.1014 | | | | | 2842 |
| 1 | –, root[c] | HPLC | 0.0294 | | | | | 2842 |
| 1 | –, root tip[c] | PBA | 4.2 | | | | | 2841 |
| | | and variation in cAMP content from top to bottom | | | | | | 2841 |
| 1 | Root | PBA | 0.309 | | | | | 2843 |

**Table 5-4** Cyclic Ribonucleotides in Plants—cont'd

| No. | Plant part | Method | cAMP | cGMP | cCMP | cUMP | cTMP | References |
|---|---|---|---|---|---|---|---|---|
| *Ziziphus jujuba* Mill (Jujube) | | | | | | | | |
| 1 | Mature fruit | RIA | 100-150 | | | | | 2844 |
| 1 | –, flesh[c] | RIA | | 30-50 | | | | 2845 |
| 1 | Mature fruit | PBA | 100-150 | | | | | 2844 |
| 1 | Immature fruit | PBA | <0.0025 | | | | | 2844 |
| *Ziziphus vulgaris*, ssp *inermis* | | | | | | | | |
| 1 | Fruit, flesh | RIA | | 19.3 | | | | 2845 |
| 1 | –, stone | RIA | | 0.14 | | | | 2845 |
| *Ziziphus vulgaris*, ssp. *spinosus* | | | | | | | | |
| 1 | Fruit, flesh | RIA | | 5.4 | | | | 2845 |
| 1 | –, stone | RIA | | 0.41 | | | | 2845 |
| | | Of some 180 medicinal herbs from China, only the fruits of *Ziziphus jujuba* and *Evodia rutaecarpa* contain cGMP[2845] | | | | | | |

nmol/g fwb unless stated otherwise.
[a]nmol/mg protein.
[b]nmol/L.
[c]Dry weight basis.
[d]nmol/$10^6$ protoplasts.
[e]nmol/mg chlorophyll.

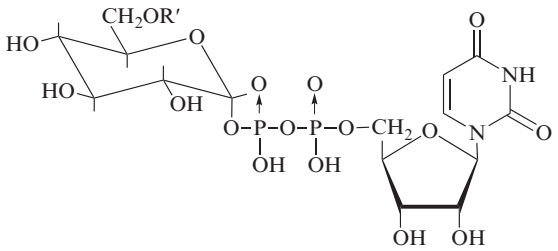
# Sugar Nucleotides

This group comprises the sugar derivatives of three of the four ribonucleoside diphosphates (ADP, GDP, and UDP) and one deoxyribonucleoside diphosphate (TDP), and related compounds such as their hexosamine and hexuronic acid derivatives. The following is a complete list of the sugar nucleotides (NDPX, where X is the sugar component) mentioned in this section:

| Nucleotide | Sugar, XH |
|---|---|
| ADP | D-Glucose (Glc),[a] D-galactose (Gal), D-fructose (Fru), D-mannose (Man), D-ribose (Rib), L-arabinose (Ara), D-xylose (Xyl), *N*-acetyl-D-glucosamine (GlcNAc) |
| GDP | D-Glucose (Glc), D-galactose (Gal), D-mannose (Man), D-rhamnose (Rha), D-ribose (Rib), D-xylose (Xyl), L-arabinose (Ara), D-fucose (Fuc) |
| CDP | None |
| UDP | D-Glucose (Glc), D-galactose (Gal), D-fructose (Fru), D-rhamnose (Rha), D-mannose (Man), D-digitoxose, D-ribose (Rib), L-arabinose (Ara), D-xylose (Xyl), D-fucose (Fuc), D-apiose (Api), D-glucuronic acid (GlcA), D-galacturonic acid (GalA), *N*-acetyl-D-glucosamine (GlcNAc), *N*-acetyl-D-galactosamine (GalNAc) |
| TDP | D-Glucose (Glc), D-galacturonic acid (GalA) |

[a]Frequently abbreviated to G, but given throughout this section as Glc to avoid any uncertainty.

Since this class of compounds is so large, the only compound whose chemistry is described in any detail is its predominant member, UDPGlc. The coverage in Table 5-6, however, is intended to be comprehensive:




**UDPGlc**

## Occurrence

UDPGlc and UDPGal were first isolated from sugar beet by Buchanan *et al.* in 1953[3344] and shown to be identical with the compounds isolated by Leloir from yeast. In 1956 Ginsburg *et al.*,[2433] who were mentioned at the beginning of this chapter in connection with the parent nucleotides, were able to identify UDPGlc, UDPGal, UDPXyl, and UDPAra (66:28:4:2) in one fraction of an extract of mung beans. In 1957 Solms and Hassid identified UDPGlcNAc and UDPGlcA in mung beans.[3377] Many other sugar nucleotides were discovered in plants over the next two decades, the majority being derivatives of UDP. The metabolic pathways for the biosynthesis of the uridine sugar nucleotides are outlined in Fig. 5-4. For a more complete review, see Feingold.[2426]

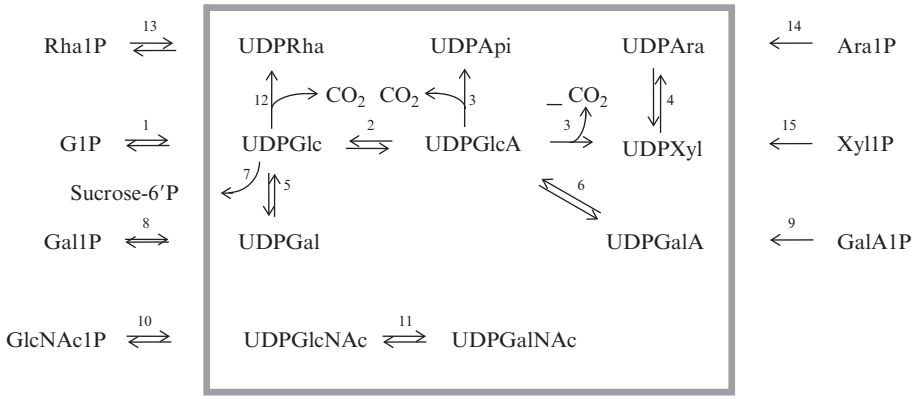



**FIGURE 5-4 Uridine Sugar Nucleotides.** (1) UDPGlc pyrophosphorylase [E.C. 2.7.7.9], UTP. (2) UDPGlc dehydrogenase [E.C. 1.1.1.22]. (3) UDPGlcA decarboxylase [E.C. 4.1.1.35]. (4) UDPXyl 4-epimerase [E.C. 5.1.3.5]. (5) UDPGlc 4-epimerase [E.C. 5.1.3.2]. (6) UDPGlcA 4-epimerase [E.C. 5.3.3.6]. (7) Sucrose synthase [E.C. 2.4.1.13] (8) UDPGal pyrophosphorylase [E.C. 2.7.7.10], UTP. (9) UDPGalA pyrophosphorylase, UTP. (10) UDPGlcNAc pyrophosphorylase, UTP. (11) UDPGlcNAc 4-epimerase.

## Separation and Analysis

### *(1) Paper Chromatography (PC) Method*

Two-dimensional PC using the solvents and conditions outlined in Chapter 1, pp 2-3, can be used to separate the sugar nucleotides from the other nucleotides, but UDPGlc is slightly degraded by solvents A2 and B2.[9,327] An alternative procedure, which can also be used for the separation of ADPGlc from the other nucleotides,[3369] is that of Paladini and Leloir[3382] in which ethanol/1*M* ammonium acetate, pH 7.5 (70:30) (solvent N2), is used in one direction followed by ethanol/1*M* ammonium acetate buffer, pH 3.8 (70:30), in the opposite direction. Dankert *et al.*[2755] published a list of PC solvent systems that can be used to separate intact UDPGlc, UDPGal, UDPGlcNAc, and UDPGalNAc from each other and of intact ADPGlc, ADPGal, ADPMan, and ADPGlcNAc from each other; all of these were found in sweet corn grains after separation of the UDP-sugar and ADP-sugar fractions by IEC.[2755] Even better separations are achieved with solvents containing organic borates.[3383] In most cases, however, it is more convenient to split the sugars from the sugar nucleotides by brief (15 min) hydrolysis at pH 2, after which the individual sugars can be separated and quantitated by PC, PE, TLC, etc., and identified by the usual tests.

### *(2) Thin-Layer Chromatography (TLC) Method*

Two-dimensional TLC separations of the sugar nucleotides are often carried out under the conditions described by Bieleski,[36] using the same solvents (B2 and A2) as those used for PC. In general, the TLC results parallel those of the PC method.

### *(3) Electrophoretic Methods*

Paper electrophoresis (PE) and thin-layer electrophoresis (TLE) have been employed occasionally in the first or second dimension of a two-dimensional PC/PE[331,337,2723] or TLC/TLE[36] chromatographic separation. The mobility $M_{AMP}$ relative to AMP = 100 is 185 for UDPGlc and 151 for ADPGlc in citrate buffer (pH 4.8).[2723]

### *(4) Ion Exchange Chromatography (IEC) Method*

This method, developed by Bergkvist[2432] and Ginsburg *et al.*[2433] in 1956, is often used to separate the sugar nucleotides from other nucleotides prior to their separation from each other. Upon IEC on an anion exchange column such as Dowex 1-X8 (formate) and a formic acid/ammonium formate gradient, the ADP sugars (ADPX) elute as a band just ahead of ADP and the UDP sugars (UDPX) elute as another band just ahead of UDP. The addition of boric acid to the gradient eluent produces a dramatic change in the elution profile allowing the ADPX and UDPX bands to elute before any of the other nucleotides,[2754] yet this simple modification of the procedure has seldom been adopted.

### *(5) High-Performance Liquid Chromatography (HPLC) Method*

This method, introduced by Liu and Shannon[342] and Carpita and Delmer[2571] in 1981, provides much higher resolution than the IEC method, but it is still not sufficient to ensure

complete separation of the sugar nucleotides. With rare exceptions, the separation is carried out in the ion-exchange mode with strongly anionic supports such as Partisil 10 SAX or Hypersil APS. In general, the sugar nucleotides are well separated according to their nucleobases, eluting in the order CDPG > UDPG > ADPG > GDPG between the nucleoside monophosphates and the nucleoside diphosphates, but the separation of compounds having similar or epimeric sugar moieties is difficult. UDPGlc and UDPGal are poorly separated but the corresponding uronic acids (UDPGlcA and UDPGalA) are well separated, appearing slightly before GDP. Another well-resolved peak eluting just before UDPGlc was identified as UDP-*N*-acetylglucosamine (UDPGlcNAc) based on its retention time, coelution with an authentic sample and UV analysis, but the presence of small amounts of UDP derivatives containing other *N*-acetylated amino sugars could not be excluded.[2440] The separation of UDPGlc and ADPGlc from each other and from other nucleotides has also been carried out by HPLC in the ion-pair mode with reversed phase supports such as Lichrosorb RP-18[2623] or Adsorbosphere.[3379]

## Analysis Without Separation

### *(1) Enzymatic Methods*

#### (A) URIDINE DIPHOSPHATE SUGARS

UDPGlc may be assayed directly without separation from other nucleotides by either of the enzymatic reactions listed in Table 5-5, the only requirement being the removal of substances that interfere with the spectrophotometric analysis. The following is a typical procedure for reaction (1):

> *For the analysis of UDP-glucose, a 25 μl sample [of a 0.5 ml barley leaf extract containing 100 mM Tris-HCl (pH 8.0) and 10 mM $MgCl_2$] was added to 0.95 ml assay solution containing 350 mM glycine (pH 8.7), 6 mM EDTA, and 0.12 IU UDP-glucose dehydrogenase. Assays were initiated by the addition of 2.1 mM $NAD^+$ and increased absorbance was measured at 340 nm.*
>
> Sicher, R. C.; Kremer, D. F; Harris, W. G., "Control of Photosynthetic Sucrose Synthesis in Barley Primary Leaves. Role of Fructose 2,6-Bisphosphate", *Plant Physiol.* **1986**, *82*(1), 15–18,[3358] reprinted by permission of the American Institute of Plant Biologists, © 1986.

This procedure can be used as the first step in a sequence of enzyme-coupled reactions in which UDPGlc, UTP, UDP, and UMP are assayed in turn in a single run (see p 296).[3027] Alternatively, UDPGlc may be assayed as the next to last step in a sequence of enzyme-coupled reactions in which G6P, F6P, G1P, ATP, UDPGlc, and ADPGlc are assayed in turn

**Table 5-5** NAD(P) Coupled Reactions

| Method | Reaction | For analysis of |
|---|---|---|
| 1 | UDPGlc + NAD → UDPGlcA + NADH | UDPGlc |
| 2 | UDPGlc + NADP → G1P + $PP_i$ | UDPGlc |

Enzymes: (1) UDPGlc dehydrogenase [E.C. 1.1.1.22]. (2) UDPGlc pyrophosphorylase [E.C. 2.7.7.9].

in a single run (see Chapter 1, p 39). This sequence uses reaction (2) to assay the UDPGlc, as in the following procedure:

> *The assay mixture (1.5 mL) in the cuvette contained the following: buffered extract [of wheat grain], 0.5 mL; Tris-HCl buffer (pH 7.8), 60 μmol; $MgSO_4$, 10 μmol; NADP, 1 μmol; sodium pyrophosphate, 3 μmol. The absorbance ($E_1$) at 340 nm was recorded. Two units (5 μL) of G-6-P dehydrogenase was added and the increased absorbance ($E_2$) noted. The extinctions $E_3$, $E_4$, $E_5$, $E_6$, and $E_7$ were likewise recorded after successive additions of 2 units (5 μL) each of phosphoglucoisomerase, phosphoglucomutase, hexokinase, UDPG pyrophosphorylase, and 5 μL of ADPG pyrophosphorylase. From these values, concentrations were calculated as $\Delta OD(G\text{-}6\text{-}P) = E_2 - E_1$, $\Delta OD(F\text{-}6\text{-}P) = E_3 - E_2$, $\Delta OD(G\text{-}1\text{-}P) = E_4 - E_3$, $\Delta OD(ATP) = E_5 - E_4$, $\Delta OD(UDPG) = E_6 - E_5$, and $\Delta OD(ADPG) = E_7 - E_6$.*
>
> Reprinted with permission from Kumar, R.; Singh, R., "Levels of Free Sugars, Intermediate Metabolites and Enzymes of Sucrose–Starch Conversion in Developing Wheat Grains", *J. Agric. Food Chem.* **1984**, *32*(4), 806–808,[548] © 1984 American Chemical Society.

**(B) ADENOSINE DIPHOSPHATE SUGARS**

ADPGlc may be assayed by the method just described.

*(2) Firefly Luminescence Method*

This method is similar to the bioluminescence method for the determination of UTP (see p 297) except that the plant extract is incubated with UDPGlc pyrophosphorylase and excess $PP_i$ (method 2, Table 5-5) instead of excess G1P prior to treatment with NDPK and ATP[2849]:

$$[\text{UDPGlc}] = [\text{ATP}]_{\text{endogenous}} + [\text{ATP}]_{\text{NDPK}} - [\text{ATP}]_{\text{pyrophosphorylase}}$$

If the assay is repeated with a mixture of UDPGlc pyrophosphorylase and UDPGal epimerase in the first incubation, the amount of UDPGal in the extract can be calculated by the expression[481]:

$$[\text{UDPGal}] = [\text{ATP}]_{\text{endogenous}} + [\text{ATP}]_{\text{NDPK}} + [\text{ATP}]_{\text{pyrophosphorylase}} - [\text{ATP}]_{\text{epimeraase}}$$

*(3) $^{31}P$ Nuclear Magnetic Resonance (NMR) Method*

Because of molecular asymmetry, the sugar diphosphate nucleotides display separate resonances for the two phosphorus atoms in their $^{31}P$ NMR spectra, further split into a pair of doublets owing to P—O—P coupling. The chemical shifts (relative to 85% phosphoric acid) are −10.38 and −11.94 ppm for UDPGlc, −10.34 and −11.83 ppm for UDPGal, −10.74 and −13.05 ppm for UDPMan, and −10.57 and −12.22 ppm for UDPGlcNAc.[68] The principal sugar nucleotides, UDPGlc and UDPGal, are readily identifiable in the $^{31}P$ NMR spectra of perchloric acid extracts of maize root tips,[587] spinach leaves and intact chloroplasts,[50] and sycamore cell suspension cultures,[3341] but in the *in vivo* studies which comprise the majority of those listed in Table 5-6 the resolution is insufficient to

**Table 5-6** UDPGlc and Other Sugar Nucleotides in Plants

| No. | Plant part | Method | UDPGlc | Other NDPX | Total | References |
|---|---|---|---|---|---|---|
| *Acer pseudoplatanus* L. (Sycamore Maple) | | | | | | |
| 1 | Cell suspension culture[a] | IEC | 90 | UDPGal trace, UDPGalA trace | | 2447 |
| 1 | Cell suspension culture[a] | $^{31}$P NMR | + | UDPGal + | | 3341 |
| *Actinidia deliciosa* Liang and Ferg. (Kiwi) | | | | | | |
| 1 | Fruit | Enzym. | 40 | | | 222 |
| 1 | Callus culture | $^{31}$P NMR | + | | | 475 |
| *Allium porrum* L. (Leek) | | | | | | |
| 1 | Seed embryo[b] | HPLC | 0.23 | | | 2458 |
| *Amorphophallus konjac* C. Koch (Konjak) | | | | | | |
| 1 | Corm[c] | IEC | 57 | ADPGlc 19, GDPMan 24 | | 3342 |
| *Apium graveolens* L. ssp. *dulce* (Celery) | | | | | | |
| 1 | Petiole, vascular bundle | PC/PC | + | | | 227 |
| *Arum maculatum* L. (Cuckoopint) | | | | | | |
| 1 | Spadix | HPLC | 292 | ADPGlc 28.8 | | 3343 |
| *Avena sativa* L. (Oats) | | | | | | |
| 1 | Seedling | IEC | 73.4 | | | 2510 |
| 1 | –, root, and stem | IEC | + | ADPGlc + | | 2475 |
| 1 | –, aerial parts | IEC | 38 | UDPGlcNAc 12 | | 2471 |
| *Beta vulgaris* L. (Sugar Beet) | | | | | | |
| 2 | Seed embryo[b] | Lumin. | 0.206-0.245 | UDPGal 0.81-0.93 | | 2478 |
| 1 | Leaf | PC/PC | + | UDPGal + | | 3344 |
| 1 | Leaf | IEC | 13.9 | | | 2479 |
| 1 | –, vascular bundle | IEC | 20.7 | | | 2479 |
| 1 | –, petiole, and parenchyma | IEC | 8.0 | | | 2479 |
| 2 | Axis[b] | Lumin. | 0.15-0.20 | UDPGal 0.15 | | 481 |
| 1 | Root[d] | IEC | 3386.8 | | | 2485 |
| 1 | Root | IEC | | UDPX (X = Glc, Gal, Xyl) 18, TDPX (X = Glc, GalA) +, GDPGlc + | | 3345 |
| *Brassica campestris* L. (Turnip Rape) | | | | | | |
| 1 | Pod, deseeded[a] | Enzym. | 136 | ADPGlc 60 | | 238 |

**Table 5-6** UDPGlc and Other Sugar Nucleotides in Plants—cont'd

| No. | Plant part | Method | UDPGlc | Other NDPX | Total | References |
|---|---|---|---|---|---|---|
| *Brassica oleracea* L. ssp. *italica* Plenck. (Broccoli) | | | | | | |
| 1 | Stems and florets | HPLC | 216 | ADPRib 0 | | 2441 |
| *Brassica pekinensis* (Lour.) Rupr. (Chinese Cabbage) | | | | | | |
| 1 | Petiole, vascular bundle | PC/PC | + | | | 227 |
| 1 | Petiole, vascular bundle | TLC/TLC | + | | | 36 |
| 1 | Petiole, vascular bundle | TLC/TLE | + | | | 36 |
| *Brassica rapa* L. (Turnip) | | | | | | |
| 1 | Leaf, vascular bundle | TLC/TLC | + | UDPX + | | 240 |
| *Bryophyllum tubiflorum* Harv. (Chandelier Plant) | | | | | | |
| 1 | Phyllodia | TLC/TLC | + | | | 3346 |
| *Camellia sinensis* L. ssp. *assamica* (Mast.) Kitam. (Assam Tea) | | | | | | |
| 1 | Leaf | IEC | 50 | | | 2500 |
| *Capsicum annuum* L. (Bell Pepper) | | | | | | |
| 1 | Leaf, mature | HPLC | 29 | | | 2503 |
| 1 | –, young | HPLC | 183 | | | 2503 |
| 1 | –, petiole | HPLC | 19 | | | 2503 |
| *Carthamus tinctorius* L.(Safflower) | | | | | | |
| 1 | Leaf | HPLC | 13 | | | 2503 |
| 1 | Flower bud | HPLC | 51 | | | 2503 |
| *Catharanthus roseus* (L.) G. Don (Madagascar Periwinkle) | | | | | | |
| 1 | Cell suspension culture | HPLC | 95 | UDPGal 4, UDPXyl 0.3, UDPAra 3, UDPGlcA 18 | | 3347 |
| 1 | Cell suspension culture | $^{31}$P NMR | + | | | 2507 |
| *Chenopodium rubrum* L. (Red Goosefoot) | | | | | | |
| 1 | Cell suspension culture | Enzym. | 40 | | | 2509 |
| *Cichorium intybus* L. (Chicory) | | | | | | |
| 1 | Root | | + | No others present | | 3348 |
| *Citrus sinensis* (L.) *Osbeck* (Orange) | | | | | | |
| 1 | Fruit, juice | IEC | + | | | 248 |

[a]Dry weight basis. [b]nmol/plant part. [c]Percent of total sugar nucleotide. [d]μg/g. [e]nmol/mL. [f]μmol/mg chlorophyll. [g]Percentage of total free nucleotide. [h]mol/mol CABP binding site. [i]μmol/mg protein. [j]nmol/mg starch.

*Continued*

**Table 5-6** UDPGlc and Other Sugar Nucleotides in Plants—cont'd

| No. | Plant part | Method | UDPGlc | Other NDPX | Total | References |
|---|---|---|---|---|---|---|
| *Cucumis sativus* L. (Cucumber) | | | | | | |
| 1 | Cotyledon[c] | HPLC | 73.15 | UDPGal 6.40, UDPXyl 0.89, UDPRha 0.58, UDPAra 1.53, UDPMan 1.27, UDPGlcA 16.18 | 0.68 | 3349 |
| 1 | Leaf | IEC | 66.0 | UDPX 81.5, ADPGlc 0 | | 250 |
| *Cucurbita maxima* Duch. (Squash) | | | | | | |
| 1 | Leaf, sieve-tube exudate | TLC/TLC | + | | | 240 |
| *Cucurbita pepo* L. (Pumpkin) | | | | | | |
| 1 | Stem, phloem exudate[e] | IEC | 758 | | | 251 |
| 1 | Ripe fruit, phloem exudate[e] | IEC | 15 | | | 251 |
| 1 | Unripe fruit, phloem exudate[e] | IEC | 343 | | | 251 |
| *Cuscuta reflexa* Roxb. (Dodder) | | | | | | |
| 1 | ? | TLC/TLC | + | | | 33 |
| *Dahlia pinnata* (Dahlia) | | | | | | |
| 1 | Tuber | IEC | + | UDPGal +, UDPFru +, UDPGalNAc + | | 3350 |
| *Datura inoxia* Mill. (Downy Thorn Apple) | | | | | | |
| 1 | Cell suspension culture | HPLC | 102* | UDPGlcNAc 4.1, UDPGlcA 4.8, UDPGalA 0.6 | | 2440 |
| | *Incl. UDPGal | | | GDPGlc (previous day) 1.7 | | 3351 |
| 1 | Cell suspension culture | HPLC | 199.1 | ADPGlc 6.6 | | 2535 |
| *Daucus carota* L. (Carrot) | | | | | | |
| 1 | Cell suspension culture | HPLC | 220 | | 450 | 2538 |
| 1 | Cell suspension culture | $^{31}$P NMR | + | | | 2507 |
| *Digitalis purpurea* L. (Digitalis) | | | | | | |
| 1 | Leaf | PC | + | UDPDigitoxose 2.8, UDPGal +, UDPAra +, UDPXyl + | 360 | 3352 |
| *Drimys lanceolata* (Poir.) Baill. | | | | | | |
| 1 | Leaf | IEC | | ADPX 17.65 | | 2543 |
| *Egeria densa* Planch. (Brazilian Waterweed) | | | | | | |
| 1 | ? | TLC/TLC | + | | | 33 |

**Table 5-6** UDPGlc and Other Sugar Nucleotides in Plants—cont'd

| No. | Plant part | Method | UDPGlc | Other NDPX | Total | References |
|---|---|---|---|---|---|---|
| *Fragaria* spp. (Strawberry) | | | | | | |
| 1 | Leaf | IEC | 90.5 | UDPGal 20.9, UDPXyl 8.4, UDPAra 10.9, UDPFru 24.3, UDPGlcA 4.2, GDPGlc 0.03, GDPGal 0.03, GDPMan 1.15, GDPXyl 0.29 | | 259 |
| 1 | Leaf | Enzym. | 106 | | | 2500 |
| *Glycine max* (L.) Merr. (Soybean) | | | | | | |
| 1 | Seed | IEC | 2.5 | | | 2553 |
| 1 | Leaf[f] | HPLC | 79 | ADPGlc 15 | | 26 |
| 1 | Root nodule | $^{31}$P NMR | + | | | 2563 |
| 1 | Sprout | PC | + | UDPGal + | | 3353 |
| 1 | Cell suspension culture | IEC | 102 | UDPGal 34, UDPXyl 2.4, UDPAra 2.4, UDPRha 1.9, ADPGlc +, ADPRib +, ADPAra +, GDPGlc +, GDPMan +, GDPAra +, GDPFuc + | 740 | 3354 |
| 1 | Cell suspension culture[e] | HPLC | 6.1 | ADPGlc 0.43 | | 3343 |
| *Gossypium arboreum* L. (Tree Cotton) | | | | | | |
| 1 | Boll, primary wall fiber[b] | IEC | 145 | UDPGal 32, UDPXyl 10, UDPAra 12, UDPGalA 18 | 218 | 2566 |
| 1 | –, secondary wall fiber[b] | IEC | 250 | UDPGal 28 | 278 | 2566 |
| *Gossypium hirsutum* L. (Upland Cotton) | | | | | | |
| 1 | Boll[b] | Enzym. | 200 | | | 2571 |
| 1 | –, fiber[g] | HPLC | >75 | UDPGal 13, UDPMan trace, UDPRha trace, UDPFuc trace, UDPXyl +, UDPAra + | | 2571 |
| 1 | Seedling, leaf | IEC | 246 (incl. UDP) | | | 2572 |
| 1 | –, chloroplast | | + | UDPGal +, ADPMan +, GDPGlc +, GDPAra + | | 2570 |
| 1 | –, root | IEC | 438 (incl. UDP) | | | 2572 |
| *Helianthus annuus* L (Sunflower) | | | | | | |
| 1 | Leaf | IEC | + | | | 3355 |
| 1 | Stem | $^{31}$P NMR | + | | | 2563 |
| *Helianthus tuberosus* L. (Jerusalem Artichoke) | | | | | | |
| 1 | Tuber | IEC | 7.75 | UDPGal 0.78, UDPFru 0.13, UDPHexNAc 0.6, GDPMan 0.9 | | 2576,3356 |
| 1 | Young stolon | IEC | + | | | 45 |

[a]Dry weight basis. [b]nmol/plant part. [c]Percent of total sugar nucleotide. [d]μg/g. [e]nmol/mL. [f]μmol/mg chlorophyll. [g]Percentage of total free nucleotide. [h]mol/mol CABP binding site. [i]μmol/mg protein. [j]nmol/mg starch.

*Continued*

**Table 5-6** UDPGlc and Other Sugar Nucleotides in Plants—cont'd

| No. | Plant part | Method | UDPGlc | Other NDPX | Total | References |
|---|---|---|---|---|---|---|
| *Hemerocallis* spp. (Daylily) | | | | | | |
| 1 | Flower petal[g] | TLC/TLC | 16.7 | ADPGlc 2.9 | | 266 |
| *Heracleum sosnowski* Manden (Cow Parsnip) | | | | | | |
| 1 | Vascular bundle, phloem | PC/PC | 40 | ADPGlc 16, UDPGal +, UDPPentose + | 104 | 2577 |
| 1 | –, xylem | PC/PC | + | ADPGlc 0, UDPGal +, UDPPentose + | 88 | 2577 |
| *Hordeum vulgare* L. (Barley) | | | | | | |
| 1 | Seed | IEC | + | | | 3357 |
| 2 | Immature grain, dehusked | Enzym. | 9-12 | | | 502 |
| 1 | Leaf[f] | Enzym. | 50 | and variation during the daily cycle | | 3358 |
| 1 | Root | HPLC | 1177 | | | 2587 |
| 1 | Root | $^{31}$P NMR | + | | | 2589 |
| 1 | Seedling, aerial parts | IEC | 44 | UDPGlcNAc 14 | | 2471 |
| *Impatiens balsamina* L. (Garden Balsam) | | | | | | |
| 1 | Leaf node | IEC | | UDPFru + | | 3359 |
| *Ipomoea batatas* (L.) Lam. (Sweet Potato) | | | | | | |
| 1 | Root | IEC | 68.1 | ADPGlc 5.9 | | 2592 |
| *Isoetes duriei* Bory | | | | | | |
| 1 | ? | TLC/TLC | + | | | 33 |
| *Lactuca sativa* L. (Lettuce) | | | | | | |
| 1 | Seed | HPLC | + | | | 2598 |
| *Larix decidua* Mill. (European Larch) | | | | | | |
| 1 | Cambial tissue | IEC | 9.1 | UDPGal 1.0, UDPXyl 1.2, UDPAra 0.7, UDPFru 0.3, ADPGlc 4.3, UDPGalA 0.3, ADPRib 0.1, ADPGal trace, ADPFru trace, GDPG 1.4, GDPGal 0.2, GDPMan 1.2 | 22.1 | 2601 |
| 1 | Xylem tissue | IEC | 8.4 | UDPGal 1.1, UDPXyl 0.3, UDPAra 0.2, UDPFru 1.5, ADPG 1.3, ADPRib 0.7, ADPGal 0.1, ADPFru 0.2, GDPG 0.3, GDPGal 0.3, GDPMan 0.1 | 14.6 | 2601 |
| *Leleba oldhami* (Munro) Nakai (Summer Bamboo) | | | | | | |
| 1 | Desheathed shoot | IEC | 72.5 | UDPXyl 13.8, UDPGlcNAc 2.5 (incl. UDPGalNAc) 2.5 | | 2602 |
| *Lemna gibba* L. (Gibbous Duckweed) | | | | | | |
| 1 | ? | TLC/TLC | + | | | 33 |
| *Lemna major* L. | | | | | | |
| 1 | Whole plant | TLC/TLC | + | | | 3360 |
| *Liriodendron tulipifera* L. (Tulip Tree) | | | | | | |
| 1 | Leaf | IEC | | UDPX 1.64, ADPX 10.92, GDPX 4.75 | | 2543 |

**Table 5-6** UDPGlc and Other Sugar Nucleotides in Plants—cont'd

| No. | Plant part | Method | UDPGlc | Other NDPX | Total | References |
|---|---|---|---|---|---|---|
| *Lycopersicon esculentum* Mill. (Tomato) | | | | | | |
| 1 | Leaf[a] | IEC | 540 | | | 473 |
| 1 | Leaf | IEC | | GDPGlc 2.48 | | 2613 |
| 1 | Fruit[h] | IEC | 225 | | | 2615 |
| *Magnolia grandiflora* L. (Southern Magnolia) | | | | | | |
| 1 | Leaf | IEC | | UDPX 6.72, ADPX 25.95, GDPX 35.68 | | 2543 |
| *Malus domestica* Borkh. (Apple) | | | | | | |
| 3 | Phloem exudate[g] | HPLC | 17-70 | | | 2623 |
| *Malus sylvestris* (L.) Mill. (Crabapple) | | | | | | |
| 1 | Stem, phloem tissue | PC/PC | + | | | 227 |
| *Medicago sativa* L. (Alfalfa) | | | | | | |
| 1 | Root | PC/PC | + | | | 280 |
| *Musa cavendishii* Lamb. ex Paxton (Dwarf Banana) | | | | | | |
| 1 | Peeled fruit | PC/PC | + | UDPGal trace | | 3361 |
| *Nicotiana alata* Link and Otto (Jasmine Tobacco) | | | | | | |
| 1 | Pollen tube | HPLC | 1600 | | | 3362 |
| 1 | Cell suspension culture | HPLC | 30 | | | 3362 |
| *Nicotiana tabacum* L. (Tobacco) | | | | | | |
| 1 | Leaf *Incl. UDPGal | HPLC | 23* | ADPGlc 1.1, GDPGlc 2.8, UDPGlcNAc 10.4 | | 2440 |
| 1 | Leaf, old[b] | HPLC | 67 (incl. UDPGal and UDPGlcNAc) | | | 3363 |
| 1 | Leaf, young[b] | HPLC | 132 (incl. UDPGal and UDPGlcNAc) | | | 3363 |
| 1 | Terminal bud[b] | HPLC | 73 (incl. UDPGal and UDPGlcNAc) | | | 3363 |
| 1 | Root *Incl. UDPGal | HPLC | 9.0* | UDPGlcNAc 3.3 | | 2440 |
| 1 | Apex *Incl. UDPGal | HPLC | 147* | UDPGlcA 7.1, UDPGalA 2.0, GDPGlc 5.3 | | 2628 |
| 1 | Pollen grain | $^{31}$P NMR | + | | | 2563 |

[a]Dry weight basis. [b]nmol/plant part. [c]Percent of total sugar nucleotide. [d]μg/g. [e]nmol/mL. [f]μmol/mg chlorophyll. [g]Percentage of total free nucleotide. [h]mol/mol CABP binding site. [i]μmol/mg protein. [j]nmol/mg starch.

*Continued*

**Table 5-6** UDPGlc and Other Sugar Nucleotides in Plants—cont'd

| No. | Plant part | Method | UDPGlc | Other NDPX | Total | References |
|---|---|---|---|---|---|---|
| 1 | Cell suspension culture | HPLC | 213* | GDPGlc 3.6, UDPGlcNAc 13.8, UDPGalA 0.6 | *incl. UDPGal | 2440 |
| 1 | Callus culture | IEC | 38.0 | ADPGlc 0 | | 3364 |
| *Oenanthe javanica* (Blume) DC (Chinese Celery) | | | | | | |
| 1 | Stem | PC/PC | 7.5* | UDP(D-GalA) 2.0<br>*Incl. UDPGal and UDPXyl | | 2498 |
| *Ophioglossum lusitanicum* L. (Least Adderstongue) | | | | | | |
| 1 | Leaf | TLC/TLC | + | | | 33 |
| *Ophioglossum vulgatum* L. (Southern Adderstongue) | | | | | | |
| 1 | Leaf | TLC/TLC | + | | | 33 |
| *Oryza sativa* L. (Rice) | | | | | | |
| 1 | Grain | IEC | + | ADPGlc + | | 2636 |
| 1 | –, 10 daf | IEC | 56 | | | 2635 |
| 1 | –, mid-milky stage | IEC | 100 | ADPGlc 33 | | 3365 |
| 1 | –, ripening kernel | IEC | 88.0 | ADPGlc 45.6 | | 2633 |
| 1 | Leaf and culm | IEC | + | ADPGlc trace | | 2636 |
| 1 | Shoot | $^{31}$P NMR | + | | | 2638 |
| 1 | Cell suspension culture | IEC | 32.0 | UDPGal 10.0, UDPXyl 3.1, UDPAra 4.0, UDPFuc 2.8, UDPRha 2.9, UDPRib 3.0, UDPMan 2.2, UDPGlcA 0.6, UDPGalA 0.2, ADPGlc 6.2, ADPRib 8.5, ADPXyl 0.3, ADPAra 0.4, GDPGlc 13.2, GDPXyl 14.3, GDPFuc 1.0, GDPRha 2.0, GDPRib 4.3 | 111.3 | 2641 |
| *Petroselinum crispum* (Mill.) Nym. (Parsley) | | | | | | |
| 1 | Whole plant[a] | IEC | 19.1 | UDPGal 6.1, UDPXyl 0.9, UDPAra 0.5, UDPFru 0.1, UDPRha 0.5, UDPApi 0.04 | 27.3 | 3366 |
| *Phacelia tanacetifolia* Benth. (Fiddleneck) | | | | | | |
| 1 | Seedling | $^{31}$P NMR | + | | | 2644 |
| *Phaseolus vulgaris* L. (Bean) | | | | | | |
| 1 | Leaf[g] | PC/PC | 58.2 | | | 12 |
| 1 | Leaf[h] | Enzym. | 3.8 | | | 519 |
| 1 | Mature leaf | IEC | 4.2 | GDPGlc 1.7 | | 2649 |
| 1 | Mature leaf | HPLC | 79 | (UDPGlcNAc +)[2651] | | 2652 |
| 1 | Young leaf | HPLC | 363 | | | 2652 |
| 1 | Etiolated leaf[b] | IEC | 0.5 | UDPXyl 2.1 | | 2650 |
| 1 | Leaf, petiole | IEC | 24 | ADPRib 0.5 | | 2653 |
| 1 | –, laminae | IEC | 24 | ADPRib 3 | | 2653 |
| 1 | Seedling | IEC | 51.0 | ADPGlc 5.0, ADPRib 3.5 | | 2656 |

**Table 5-6** UDPGlc and Other Sugar Nucleotides in Plants—cont'd

| No. | Plant part | Method | UDPGlc | Other NDPX | Total | References |
|---|---|---|---|---|---|---|
| 1 | Seedling, leaf | IEC | 230 | | | 2657 |
| 1 | –, root | IEC | 160 | | | 2657 |
| 1 | Fruit, pericarp | IEC | 117 | | | 520 |
| *Phyllostachys pubescens* [Mazel ex] Houz. (Moso Bamboo) | | | | | | |
| 1 | Desheathed shoot | IEC<br>*Incl. UDPGal | 24.0* | UDPXyl 7.6, UDPGalA 3.6, UDPGlcNAc 3.6 (incl. UDPGalNAc) | | 2661 |
| *Pinus banksiana* Lamb. (Jack Pine) | | | | | | |
| 1 | Seedling[g] | IEC | 1.0 | | | 2665 |
| *Pisum sativum* L. (Pea) | | | | | | |
| 1 | Seed | IEC | 216 | | | 24 |
| 1 | Seed | IEC | + | UDPGal +, UDPXyl +, UDPAra +, UDPRha +, UDPGlcNAc +, UDPGalNAc +, ADPGlc + | 217 | 3367 |
| 1 | Mature seed | IEC | 79 | ADPRib 39, UDPGal trace | | 2437 |
| 1 | Seed | HPLC | 309 | ADPRib trace | | 2441 |
| 2 | Seed embryo | HPLC | 324-421 | | | 295 |
| 1 | Seed coat | Enzym. | 496 | | | 2676 |
| 1 | Leaf[f] | HPLC | 4.2 | | | 3368 |
| 1 | Root | IEC | 3600 | | | 2683 |
| 1 | Root tip | $^{31}$P NMR | + | | | 526 |
| 1 | Seedling | PC/PC | 0 | | | 2681 |
| 1 | –, cotyledon | Enzym. | 238 | | | 527 |
| *Populus deltoides* Bartr. ex Marsh (Eastern Cottonwood) | | | | | | |
| 1 | Leaf[f] | Enzym. | 72 | | | 297 |
| *Pteridium aquilinum* (L.) Kuhn (Bracken Fern) | | | | | | |
| 1 | Rhizome[a] | IEC | 9.1 | UDPGal 2.3, UDPXyl 1.3, UDPAra 0.4, UDPGalA 0.6, GDPMan 0.9, GDPFuc 0.4 | | 2689 |
| *Ricinus communis* L. (Castor Bean) | | | | | | |
| 1 | Seedling cotyledon | Enzym. | 259 | | | 303 |
| 1 | Phloem exudate[e] | HPLC | 400 | | | 304 |
| 1 | Phloem exudate[e] | Enzym. | 450 | | | 2694 |
| *Saccharum officinarum* L. (Sugar Cane) | | | | | | |
| 1 | Leaf[g] | PC/PC | | UDPX 11.9 | | 306 |
| 1 | Stalk, third internode[i] | HPLC | 8.6 | and variation from third to ninth internode | | 307 |
| 1 | Root[g] | PC/PC | 6.1 | UDPX 4.5 | | 306 |

[a]Dry weight basis. [b]nmol/plant part. [c]Percent of total sugar nucleotide. [d]μg/g. [e]nmol/mL. [f]μmol/mg chlorophyll. [g]Percentage of total free nucleotide. [h]mol/mol CABP binding site. [i]μmol/mg protein. [j]nmol/mg starch.

*Continued*

**Table 5-6** UDPGlc and Other Sugar Nucleotides in Plants—cont'd

| No. | Plant part | Method | UDPGlc | Other NDPX | Total | References |
|---|---|---|---|---|---|---|
| *Salix triandra* L. (Almond Willow) | | | | | | |
| 1 | Phloem exudate | TLC/TLC | + | | | 309 |
| *Selaginella denticulata* (L.) Link (Tooth-Leaved Clubmoss) | | | | | | |
| 1 | ? | TLC/TLC | + | | | 33 |
| *Sinapis alba* L. (White Mustard) | | | | | | |
| 1 | ? | TLC/TLC | + | | | 33 |
| *Solanum tuberosum* L. (Potato) | | | | | | |
| 1 | Tuber | PC/PC | + | | | 9 |
| 1 | Tuber[g] | IEC | 33.2 | | | 316 |
| 1 | Tuber | Enzym. | 60 | Variation in UDPGlc content along the stolon-apex axis | | 533 |
| 1 | Tuber, mature | HPLC | 29 | | | 532 |
| 1 | –, immature | HPLC | 105 | | | 532 |
| 1 | Starch grain | IEC | 0 | ADPGlc 2.0, ADPRib 0 | | 2709 |
| *Sorghum bicolor* (L.) Moench (Sorghum) | | | | | | |
| 1 | Seed [a] | PC/PC | 1750* | *Incl. ADPGlc | 2500 | 3369 |
| 1 | Root tip | $^{31}$P NMR | + | | | 44 |
| *Spinacia oleracea* L. | | | | | | |
| 1 | Leaf[f] | Enzym. | 90 | and subcellular distribution | | 322 |
| 1 | Leaf | Enzym. | | Diurnal variation in UDPGlc | | 534 |
| 1 | Leaf | $^{31}$P NMR | + | UDPGal + (both absent in chloroplast) | | 50 |
| *Spirodela oligorrhiza* (Kurz.) Hegelm. (Duckweed) | | | | | | |
| 1 | Whole plant | TLC/TLC | + | | | 3360 |
| *Tilia platyphyllos* Scop. (Large-Leaved Linden) | | | | | | |
| 1 | Phloem exudate | TLC/TLC | + | | | 328 |
| *Tillandsia usneoides* (L.) L. (Spanish Moss) | | | | | | |
| 1 | ? | TLC/TLC | + | | | 33 |
| *Trifolium subterraneum* L. (Sub Clover) | | | | | | |
| 1 | Whole plant[a] | IEC | 250 | | | 329 |
| *Trigonella foenum-graecum* L. (Fenugreek) | | | | | | |
| 1 | Seed[a] *Incl. UDPGal | IEC | 39.2* | | | 2716 |
| 1 | Sprout[a] *incl. UDPGal | IEC | 123.8* | GDPMan 32.0 | | 2716 |
| ×*Triticosecale* Wittm. (Triticale) | | | | | | |
| 1 | Grain | IEC | 3.4* | ADPGlc 0.4, GDPGlc 0.2 *Incl. UDPGal and UDPMan | | 3370 |
| *Triticum aestivum* L. (Wheat) | | | | | | |
| 1 | Grain | IEC | 57.7 | ADPGlc 22.0 | | 2721 |

**Table 5-6** UDPGlc and Other Sugar Nucleotides in Plants—cont'd

| No. | Plant part | Method | UDPGlc | Other NDPX | Total | References |
|---|---|---|---|---|---|---|
| 1 | –, ripening kernel | IEC | 72.1 | ADPGlc 18.5 | | 2633 |
| 1 | Grain[b] | Enzym. | 16.3 | ADPGlc 8.6 | | 537 |
| 1 | Grain | PC/PE | 346 | ADPGlc 98 | | 2723 |
| 1 | –, endosperm | PC/PE | 381 | ADPGlc 162 | | 2723 |
| 1 | –, testa, pericarp | PC/PE | 230 | ADPGlc 32 | | 2723 |
| 1 | Seed, aleurone tissue | PC/PC | 90.3 | UDPFru 39.7, UDPGal 39.7, UDPXyl 34.3 | | 2724 |
| 1 | Grain, peeled | HPLC | 700 | ADPGlc 160 | | 3371 |
| 2 | Seed, embryo[a] | Enzym. | 24-36 | | | 3372 |
| 1 | Seed, embryo | HPLC | + | | | 2598 |
| 1 | Leaf[g] | PC/PC | 5.80 | | | 331 |
| 1 | Leaf[g] | PC/PE | 6.58 | | | 331 |
| 1 | Leaf[f] | Enzym. | 40 | | | 3373 |
| 1 | Flag leaf[a] | HPLC | 360 | UDPGlcNAc 150 | | 3374 |
| 1 | Shoot | $^{31}$P NMR | + | | | 2638 |
| 1 | Seedling, embryo | IEC | + | | | 2768 |
| 1 | –, leaf | PC/PC | + | | | 3375 |
| 1 | –, shoot | PC/PC | + | | | 3376 |
| 1 | Seedling, root | PC/PC | + | | | 3376 |
| 1 | –, scutellum | PC/PC | + | | | 3376 |
| 1 | –, root, and stem | IEC | + | ADPGlc ? | | 2475 |
| 1 | –, aerial parts | IEC | 27 | UDPX 4 | | 2432 |
| *Triticum compactum* Host (Club Wheat) | | | | | | |
| 1 | Leaf | IEC | + | | | 2736 |
| *Vicia faba* L. (Faba Bean) | | | | | | |
| 1 | ? | TLC/TLC | + | | | 33 |
| *Vigna mungo* (L.) Hepper (Black Gram) | | | | | | |
| 1 | Root tip[e] | $^{31}$P NMR | 620 | | | 542,543 |
| *Vigna radiata* (L.) Wilcz. (Mung Bean) | | | | | | |
| 1 | Sprout | IEC | + | UDPGal +, UDPXyl +, UDPAra +, UDPGlcNAc +, GDPMan +, UDPGalNAc +, UDPGlcA +, UDPGalA + | | 2742 |

[a]Dry weight basis. [b]nmol/plant part. [c]Percent of total sugar nucleotide. [d]µg/g. [e]nmol/mL. [f]µmol/mg chlorophyll. [g]Percentage of total free nucleotide. [h]mol/mol CABP binding site. [i]µmol/mg protein. [j]nmol/mg starch.

*Continued*

**Table 5-6** UDPGlc and Other Sugar Nucleotides in Plants—cont'd

| No. | Plant part | Method | UDPGlc | Other NDPX | Total | References |
|---|---|---|---|---|---|---|
| 1 | Seedling | IEC | 33 | UDPGal 14, UDPXyl 2, UDPAra 1, ADPRib 10 | 50 | 2433 |
| 1 | Seedling | IEC | | UDPGlcNAc 1.4, UDPGlcA 0.4 | | 3377 |
| 1 | Seedling | HPLC | 175 | ADPRib 0 | | 2441 |
| 1 | –, hypocotyl | IEC | 204 | UDPGal 28, UDPXyl trace, UDPAra trace, UDPRha 6, UDPGlcNAc 38, GDPMan trace | | 2744 |
| *Yucca flaccida* Haw. (Weak-Leaf Yucca) | | | | | | |
| 1 | Phloem exudate | TLC/TLC | + | | | 309 |
| *Zea mays* L. (Corn) | | | | | | |
| 1 | Grain, milky stage | PC/PC | | ADPGlc 8 | | 3378 |
| 1 | Grain, milky stage[g] | IEC/PC | 6.8* | ADPGlc 4.1, ADPGal 1.7, ADPMan 2.1, ADPGlcNAc 0.7 | | 2755 |
| | | *Incl. UDPGal | | UDPGlcNAc 1.5, UDPGalNAc 2.4 | | |
| 1 | Immature grain | IEC | | UDPX 220, GDPX 472 | | 2754 |
| 1 | Immature kernel, endosperm[j] | HPLC | | UDPX 17.32, ADPX 7.48 | | 342 |
| 1 | –, starch granule[j] | HPLC | | UDPX 1.91, ADPX 0.68 | | 342 |
| 1 | Grain, endosperm[a] | HPLC | 1416 | ADPGlc 596 | | 3379 |
| 1 | Leaf | PC/PE | 57 | | | 337 |
| 1 | Leaf | IEC | 1.76 | GDPGlc 1.38 | | 2613 |
| 1 | Ovary[b] | Enzym. | 0.4 | | | 343 |
| 1 | Root | PC/PC | 168 | | | 12 |
| 1 | Root | TLC/TLC | + | | | 12 |
| 1 | Root tip[b] | HPLC | 4.54 | | | 2759 |
| 1 | Root tip | HPLC | + | ADPGlc 0, UDPGlcNAc +, GDPGlc + | | 3380 |
| 1 | Root tip | $^{31}$P NMR | + | | | 544,3381 |
| 1 | Root tip | $^{31}$P NMR | + | UDPGal + | | 587 |
| 1 | Culm[b] | HPLC | 97.5 | | | 2759 |
| 1 | Seedling | IEC | 54.0 | UDPGlcNAc 1.4, UDPGlcA 0.4 | | 2656 |

nmol/g fwb unless stated otherwise.
[a]Dry weight basis.
[b]nmol/plant part.
[c]Percent of total sugar nucleotide.
[d]µg/g.
[e]nmol/mL.
[f]µmol/mg chlorophyll.
[g]Percentage of total free nucleotide.
[h]mol/mol CABP binding site.
[i]µmol/mg protein.
[j]nmol/mg starch.

distinguish between them. The sugar nucleotide under the UDPG peak could well contain UDPGal or other UDPX, though UDPGlc is usually predominant in plants. Uchiyama and Sakata,[543] however, were able to positively identify UDPGlc in mung bean root tips *in vivo* by applying the maximum entropy method (MEM) to the FT-NMR signals to obtain super-resolved $^{31}$P NMR spectra.

## Physical Properties

Uridine Diphosphate Glucose (UDPG or UDPGlc), $C_{15}H_{24}N_2O_{17}P_2$. *Uridine 5′-(Trihydrogen Diphosphate), Mono-α-D-glucopyranosyl Ester*

UDPG [R.N. 133-89-1]: White powder, $[\alpha]_D^{21} + 45°(H_2O)$, +35° (8*M* urea).[3384] Spectra: UV,[3239] $^1$H NMR (fig.),[461] $^{13}$C NMR,[405] $^{31}$P NMR,[68] ESI-MS (3:1 α:β),[422] ESI-MS/MS,[403] FAB-MS/MS.[3385] Chromatography: PC,[9] TLC,[36] HPTLC,[2891] IEC,[3365] HPLC,[2440] GFC.[3386] Electrophoresis: PE,[9] TLE,[36] capillary isotachophoresis,[3239] CZE,[3387] MECC.[3387]

$Na_2C_{15}H_{22}N_2O_{17}P_2$ [R.N.117756-22-6]: FAB-MS,[2911] SI-MS.[3388] *Dihydrate* [R.N. 89705-69-1]: Monoclinic platelike crystals, $d_m$ 1.80, $d_c$ 1.796, X-ray structure[419]; laser Raman spectrum.[3389]

$Li_2C_{15}H_{22}N_2O_{17}P_2 \cdot 6H_2O$: White powder. PC, PE.[3390]

## Conformation

UDPG takes the extended form both in the crystal[419] and in solution.[3391] In the crystalline state the conformation about the *N*-glycosidic bond is *anti*, the ribose is C(2′)-*endo* ($^2$E), and the pyrophosphate linkage takes a staggered form.[419] Kim, however, suggests that UDPG has a folded conformation with the glucosyl 2- and 3-OH groups located inside the folded structure, based on the relative reactivity of the OH groups toward acylation and supported by semiempirical and *ab initio* energy calculations.[3392]

## Synthesis

UDPG may be prepared (a) from UMP in poor yield by condensation with glucose 1-phosphate (G1P) in the presence of dicyclohexyl carbodiimide,[3393] (b) from a UMP ester,[3394] thioester,[3395] morpholide,[3390,3396] triazolide,[3397] anhydride,[2989] or UMP derivative containing 2′,3-OH protective substituents[3398,3399] by condensation with G1P in pyridine, (c) from UDP by condensation with 2-(β-D-glucosyloxy)-3-methoxypyridine in DMF,[422] (d) from the *O,O*-diphenyl ester of UDP by displacement of the terminal phosphate group with G1P,[3010] or (e) from UTP and G1P by the action of coupled enzymes.[3072]

## Hydrolysis

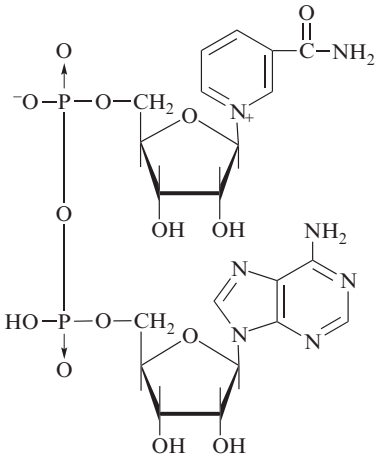
UDPG is stable in buffered aqueous solution at neutral pH but decomposes at high pH[3382] or in the presence of Mn(II) and other metal ions[3400] giving UMP and glucose 1,2-cyclic phosphate. The rate of hydrolysis at pH 2.70 and 20 °C is $2.5 \times 10^{-6}$ min$^{-1}$, which corresponds to a half-life of 20 days.[3401] The standard free energy change $\Delta G'^{\circ}$ for the hydrolysis of UDPG to UMP and G1P, based on the −7.3 kcal/mol value reported by Avigad[262] for the hydrolysis of UDPG to UDP and glucose, was calculated to be −10.3 kcal/mol at pH 7.0 and 25 °C.[3402]

# 6 Dinucleotides

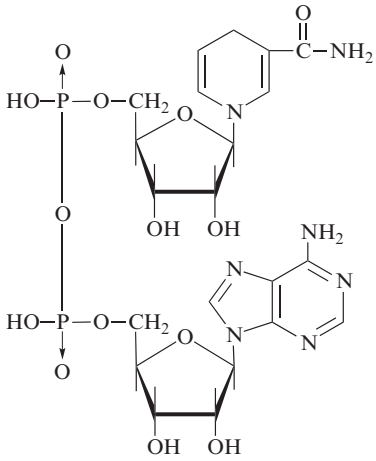
This group comprises the pyridine adenine dinucleotides NAD and NADP, the riboflavin adenine dinucleotide FAD, and their respective dihydro derivatives. The pyridine dinucleotides are considered first.

## Pyridine Adenine Dinucleotides

This group comprises the dinucleotides NAD, NADP and their dihydro derivatives NADH and NADPH.



**NAD**, X = H
**NADP**, X = $P(O)(OH)_2$



**NADH**, X = H
**NADPH**, X = $P(O)(OH)_2$

### Nomenclature

The coenzyme NAD was originally (1923) called cozymase, then codehydrogenase I, coenzyme I (CoI), or diphosphopyridine nucleotide (DPN, 1936). Its current name, nicotinamide adenine dinucleotide (NAD), was adopted by the IUB in 1960.[3403] The charged symbol $NAD^+$ currently in vogue is not sanctioned by the IUB and should be discouraged because, as Alberty pointed out,[3404] NAD actually has a negative charge in the neutral pH range in which it normally exists. Similar comments apply to the coenzyme NADP, previously called codehydrogenase II, coenzyme II (CoII), or triphosphopyridine nucleotide (TPN).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## Occurrence

The first reports of the occurrence of coenzymes I and II in the higher plants were those of von Euler and Nordenfelt,[3405] who isolated coenzyme I from barley root tips in 1926 and Whatley,[3406] who isolated coenzyme II from the leaves and other tissues of clover, chickweed, oats, potato, elder, and runner beans in 1951. The chemical structures of the two coenzymes were both known by 1950. Although it had been long known that the reduced coenzymes NADH and NADPH could be extracted without degradation from yeast or animal tissue by dilute alkali, they were not isolated from plants until the early 1960s. NADPH was isolated in 1961 from peas by Marré and Bianchetti,[3407] and NADH and NADPH were isolated in 1963 from corn, tobacco, and various other plants by Fritz *et al.*,[3408] Sunderland and Merrett,[3409,3410] and Yamamoto,[3411] respectively.

The function of these coenzymes in plants, as in animals and bacteria, is to act as redox reagents for a broad variety of metabolic reactions. As a general rule, the NADP/NADPH couple functions in synthetic (anabolic) reactions and the NAD/NADH couple functions in degradative (catabolic) reactions.[3412] The two couples are usually found in separate compartments within the plant cell. In the leaf, for example, the NADH/NADPH couple resides within the chloroplast and the NAD/NADH couple in the cytosol.[3413]

The metabolic pathways for the biosynthesis of the dinucleotides are outlined in Fig. 6-1. NAD and its precursors nicotinic acid mononucleotide (NAMN) and nicotinic acid adenine dinucleotide (NAAD) are components of the pyridine nucleotide cycle.[3414] NAAD, synthesized from NAMN by reaction with ATP, is converted to NAD by amidation with glutamine (step 1). Cleavage of the pyridine-ribose bond (step 2) yields ADP-Ribose and nicotinamide. Deamidation of the nicotinamide to nicotinic acid and reaction of the latter with R5P to form NAMN completes the cycle. In step 3, NAD is reversibly phosphorylated by ATP giving NADP, this being the only known mechanism for the biosynthesis of NADP.[3411] An ATP-dependent NADH kinase [E.C. 2.7.1.86] that converts NADH to NADPH has been reported for yeasts[3415] but not yet for plants. In steps 4 and 5, NAD and NADP are reversibly reduced to NADH and NADPH, respectively, by reaction with a dehydrogenase and its substrate. About 200 dehydrogenases have been identified in plants,[3416] some (such as alcohol dehydrogenase) specific for NAD, others (such as G6P dehydrogenase) specific for NADP, and

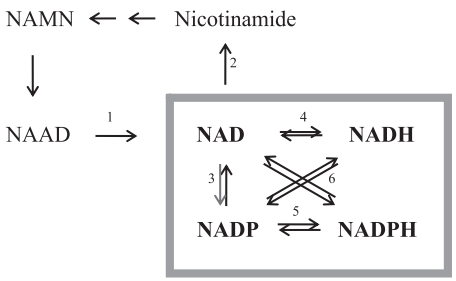



**FIGURE 6-1 Pyridine Dinucleotides.** (1) NAD synthase [E.C. 6.3.5.1], L-glutamine and ATP. (2) NAD nucleosidase [E.C. 3.2.2.5]. (3) NAD kinase [E.C. 2.7.1.23] and ATP. (4) An NAD-specific dehydrogenase and its substrate, for example, alcohol dehydrogenase [E.C. 1.1.1.1] and ethanol. (5) An NADP-specific dehydrogenase and its substrate, for example, G6P dehydrogenase [E.C. 1.1.1.49] and G6P. (6) Ferredoxin-NADP reductase [E.C. 1.18.1.2] and reduced ferredoxin.

still others (such as glutamate dehydrogenase) specific for both. Spinach ferredoxin-NADP reductase [E.C. 1.6.7.1] has been shown to catalyze transhydrogenation reactions among the four dinucleotides (step 6).[3417] There appears to be no enzymatic mechanism for salvage of the reduced dinucleotides other than return to their oxidized forms.

## Extraction

The conditions under which the dinucleotides can be extracted without degradation are governed by their unusually high sensitivity to pH. The oxidized compounds NAD and NADP are stable to acid and unstable to base, whereas the reduced compounds NADH and NADPH are stable to base and unstable to acid.[3418] Extraction with aqueous solutions of acids such as perchloric acid or trichloroacetic acid under the conditions normally employed for the extraction of mononucleotides can therefore only be used for the analysis of NAD and NADP although, as Brown demonstrated, the degradation products of NADH and NADPH can be used as a measure of their initial concentration.[2437] In general, however, it is preferable to extract the oxidized and reduced dinucleotides separately, as illustrated by the following example:

> *Leaves (2 g) and globe "roots" (2 g) of 25-day old radish plants were chopped up separately with a razor blade and ground in a homogenizer at 90-95 °C for 2 min with 10 ml of 0.1N HCl to extract oxidized coenzymes (NAD and NADP). Additional tissue (2 g each) was similarly treated with 0.1N NaOH to extract reduced coenzymes (NADH and NADPH). Each of the four homogenates was then rapidly chilled in ice bath and adjusted to pH 6.5 with NaOH or pH 7.5 with HCl and then 0.5 ml of 0.2 M glycylglycine buffer at pH 6.5 or pH 7.5 was added, in the case of oxidized and reduced coenzymes respectively. Total volumes were measured, and then each homogenate was centrifuged at 10,000 g for 20 min at 4 °C. Supernatants were stored frozen at −80 °C before assay of coenzymes.*
>
> Tezuka, T.; Yamaguchi, F.; Ando, Y., "Physiological Activation in Radish Plants by UV-A Radiation", *Photochem. Photobiol.* **1994**, *24B*(1), 33–40,[3419] reprinted by permission of Elsevier, © 1994.

## Separation and Analysis

### *(1) Paper (PC) or Thin Layer (TLC) Chromatography Methods*

NAD and NADP can be separated from other nucleotides and from each other by two-dimensional PC[9] or TLC[33] on methanol/chloroform/7*M* formic acid extracts, but the only quantitative data reported to date are for 2d-PC/PE separations performed on TCA extracts of developing wheat grain.[2723]

### *(2) Ion Exchange Chromatography (IEC) Method*

Under the conditions employed by Bergqvist[2471] for the separation of acid soluble nucleotides referred to in the previous chapter, NAD and NADP are well separated from each other but tend to coelute with other nucleotides. NAD elutes early under the CMP peak

and NADP later under the CDP peak.[2471] The reduced dinucleotides NADH and NADPH cannot be separated by this method because they are degraded by acidic solvents, but it has been found that their main scission products—ADP-Ribose and ADP-Ribose-2′-phosphate, respectively—are well resolved and can be taken as a measure of the initial concentration of each compound.[2437] All four dinucleotides can be separated without degradation by IEC on a DEAE-Sephadex A-25 column with LiCl gradient elution.[2894] This procedure has been used in a few instances to separate NAD and NADP from plant extracts,[2566,2654,2683] but has yet to be used for the separation of intact NADH or NADPH from plants.

*(3) High-Performance Liquid Chromatography (HPLC) Method*

This method has been used since the mid-1980s for the separation of NAD and NADP from other nucleotides in plant extracts. It can be used in the IEC mode with strongly anionic column packings such as Partisil-10 SAX[2651] or μ-Bondapak $NH_2$[2441] or in the reverse-phase (RP) mode with packings such as Hypersil ODS.[2440] NAD is eluted before NADP in the IEC mode and in the reverse order in the RP mode. Curiously, none of the studies in Table 6-2 mentions the presence of ADP-Ribose-2′-phosphate, the degradation product of NADPH, and only two of them mention the presence of ADP-Ribose, the degradation product of NADH.[2441,3494] In their studies on *Costus speciosus* cell suspension cultures, Li *et al.*[2523] circumvented this problem by using a 0.5*M* perchloric acid extract for the NAD and NADP analysis and a 0.5*M* NaOH extract for the NADH and NADPH analysis. The extracts were freeze dried, redissolved in pH 6.0 and pH 8.0 buffer, respectively, and subjected separately to HPLC on a Supelcosil LC-18 RP column and a $K_2HPO_4$/citrate (pH 4.5) mobile phase. Aso *et al.*[3417] developed a similar procedure for separating the four dinucleotides simultaneously and used it to measure the effect of each dinucleotide on the transhydrogenase activity of ferredoxin-NADP reductase [E.C. 1.18.1.2] isolated from spinach leaves, but did not determine their endogenous levels.

*(4) Fluorimetric Methods*

Bevilacqua and Scuncia[3420] used the fluorimetric method of Robinson *et al.*[3501] to measure the NAD(P) content of a wide variety of plants. In this method, a TCA plant extract containing a few milligrams of $Ce(SO_4)_2$ to oxidize any reduced NAD(P), was treated with acetone and 6N NaOH, resulting in the formation of a highly fluorescent compound ($\lambda = 360$ nm), which was measured fluorimetrically. Green leaves require an additional oxidation with permanganate prior to measurement to destroy their intrinsic fluorescence.[3421] The method was unable to distinguish between NAD and NADP and was soon superseded by the fluorimetric method of Ciotti and Kaplan,[3502] discussed later in method 7C.

*(5) Cyanide Addition Method*

Colowick *et al.*[3503] developed a spectrophotometric method suitable for the analysis of NAD and NADP based on the adduct formed when each compound is treated with 1.0*M* KCN in aqueous solution (pH 11). The UV spectra of the adducts show reduced

absorption at 260 nm and a new peak at 325 nm, much like those of NADH and NADPH, both of which show reduced absorption at 260 nm and a new peak at 340 nm. This method was applied in its original form by Brown[2437,3471] and Mangat[2655,2656] to perchloric acid extracts of various plant seeds or seedlings after fractionation by IEC, and in modified form by Pao *et al.*[3487] who extracted wheat leaves with water, precipitated the dinucleotides with acetone, and measured the cyanide adducts fluorometrically at an excitation wavelength of 325 nm and an emission wavelength of 430 nm.

### *(6) Luminometric Method*

This method utilizes the bacterial luminescence produced from NAD(P)H by the following coupled reactions:

$$\text{NAD(P)H} + \text{FMN} \leftrightarrow \text{NAD(P)} + \text{FMNH}_2 \qquad \text{Enzyme : FMN reductase[EC 1.6.8.1]}$$
$$\text{FMNH}_2 + \text{RCHO} + \text{O}_2 \leftrightarrow \text{FMN} + \text{RCO}_2\text{H} + \text{H}_2\text{O} + h\nu \qquad \text{Enzyme : Luciferase[EC 1.14.14.3]}$$

Stuhlfauth *et al.*[2540] and Krishnaraj and Thorpe[3488] used the commercial monitoring kits available for this purpose to measure the NADH and NADPH contents of *Digitalis lanata* and wheat leaves, respectively.

### *(7) Enzymatic Methods*

In this method, each of the four dinucleotides is analyzed separately using one of the enzymatic reactions listed in Table 6-1. Several procedures are available that differ primarily in the manner in which the products are detected and measured. The introduction of enzyme recycling by Lowry in 1961 brought about such a dramatic improvement in sensitivity and accuracy that almost all the analyses done since then have been carried out in the recycling mode regardless of the procedure adopted.

#### (A) MANOMETRIC METHODS

In their early studies on cozymase (NAD), von Euler *et al.*[3405,3428] measured the NAD content of various plant tissues by the amount of $CO_2$ evolved when an aliquot of the aqueous extract was added to a solution of glucose and NAD-free brewer's yeast (apozymase) in pH 4.6 phosphate buffer. The results were compared to the values obtained with authentic NAD assayed under the same conditions. Okunuki[3430] and von Euler *et al.*[3428] used this

**Table 6-1** Some NAD(P)-Linked Reactions

| No. | Reaction | Enzyme | |
|---|---|---|---|
| 1 | NAD + ethanol ↔ NADH + acetaldehyde | Alcohol dehydrogenase | [E.C. 1.1.1.1] |
| 2 | NAD + lactate ↔ NADH + pyruvate | Lactate dehydrogenase | [E.C. 1.1.1.27] |
| 3 | NAD + $PP_i$ ↔ NMN + ATP | NAD pyrophosphorylase | [E.C. 2.7.7.1] |
| 4 | NADP + glutamate + $H_2O$ ↔ NADPH | Glutamate dehydrogenase + α-ketoglutarate + $NH_3$ | [E.C. 1.4.1.4] |
| 5 | NADP + G6P ↔ NADPH + 6-PG | G6P dehydrogenase | [E.C. 1.1.1.49] |
| 6 | NADP + isocitrate ↔ NADPH | Isocitrate dehydrogenase + α-ketoglutarate + $CO_2$ | [E.C. 1.1.1.42] |

method to determine the NAD content of a wide variety of pollens. More recently, Greenbaum *et al.*[3467] developed a modified enzyme recycling method (see below) that uses an oxygen electrode inserted into the sealed reaction vessel to measure the consumption of oxygen corresponding to the rate of enzymatic reduction. All four dinucleotides can be measured at levels as low as 0.01-0.02 μg. This method has the advantage that it can be used with extracts that contain reducing, fluorescent, or colored compounds, for example, green leaves, but so far it has been used only with extracts of pea leaf,[3467] tobacco callus culture,[2630] and pineapple orange fruit juice vesicles.[3435]

**(B) SPECTROPHOTOMETRIC METHODS**

All four dinucleotides have a maximum absorption at 260 nm in their UV spectra, but the reduced dinucleotides NADH and NADPH have an additional maximum at 340 nm. Anderson and Vennesland[3458] used the increase in light absorption at 340 nm to measure the NAD and NADP contents of TCA extracts of various plant leaves using reactions 1 and 5 of Table 6-1 to reduce the dinucleotides to NADH and NADPH, respectively. Whatley[3406] developed a method for the analysis of NADP in plant tissues based on reactions 5 or 6 of Table 6-1 together with Warburg's "old yellow enzyme" and methylene blue, measurement being made by comparing the rate of disappearance of the blue color with that of authentic NADP assayed under the same conditions.

These methods soon gave way to the enzymatic cycling method introduced by Lowry in 1961. In this method, the NADH or NADPH produced in the initial reaction is reoxidized to NAD or NADP via a carrier such as phenazine methosulfate (PMS) and an acceptor such as 2,6-dichlorophenolindophenol (DCPIP) present in the reaction mixture, the reaction cycling back and forth until all of the initial dinucleotide is consumed. The method is best illustrated by an example of one of the most widely used procedures, that of Slater and Sawyer (1962).

> *The $NAD^+$ assay contained leaf extract, 32 μmoles tris-HCl (pH 7.4), 780 μmoles ethanol, 0.75 μmoles phenazine methosulphate (PMS) and 108 mμmoles DCIP in a final volume of 1.50 ml. Enzyme (50 μg Boehringer alcohol dehydrogenase) was added after temperature equilibration at 23°; water replaced enzyme in the blank. The reaction was measured by continuously recording the rate of dye reduction at 610 mμ using a Cary recording spectrophotometer. To calculate the amounts of $NAD^+$ in the leaf extracts, these rates were compared with those obtained using known amounts of $NAD^+$... NADH was estimated in a reaction mixture containing leaf extract, 25 μmoles tris–HCl (pH 7.4), 620 μmoles ethanol, 0.72 μmole PMS, and 86 mμmoles DCIP in a final volume of 1.20 ml. Complete NADH reoxidation, requiring 15 minutes, was attained before the addition of 150 μg of enzyme. Rates were compared with those obtained using [known amounts of] NADH. The $NADP^+$ assay contained leaf extract, 30 μmoles tris-HCl (pH 7.4), 3 μmoles glucose-6-P, 0.60 μmole PMS, 86 mμmoles DCIP, and 2 μmoles EDTA. The total volume was 1.20 ml. After a period of temperature equilibration, 5 μg of enzyme (Boehringer glucose-6-P dehydrogenase) was added. These rates were compared with those obtained using [known amounts of] $NADP^+$... NADPH was estimated in a reaction mixture containing leaf*

*extract, 34 μmoles tris–HCl (pH 7.4), [3.4 μmoles G6P], 0.72 μmole PMS, and 142 mμmoles DCIP in a total volume of 1.30 ml. To increase reaction rates, the concentrations of PMS and DCIP were higher than those used in $NADP^+$ assays; EDTA was excluded. Enzyme (6.2 μg) was added after a reoxidation period of 25 minutes. Rates were compared with those obtained using [known amounts of] NADPH.*

Ryrie, I. J., and Scott, K. J., "Changes in Nicotinamide Nucleotide Coenzymes in Barley Leaves Infected with Powdery Mildew", *Plant Physiol.* **1968**, *43*(5), 687–692,[3447] reprinted by permission of the American Society of Plant Biologists, © 1968.

Several modifications of this procedure are available. In the modification described by Yamamoto,[3411] phenazine methosulfate is replaced as the carrier by NAD diaphorase (for NADH) or NADP diaphorase (for NADPH), other conditions remaining the same. In the modification of Lechevallier *et al.*,[3485] the carrier is phenazine ethosulfate (PES) and DCPIP is replaced as the acceptor by thiazolyl blue, monitored at 570 nm, other conditions remaining the same. Both of these modified procedures have been widely used.

**(C) FLUORIMETRIC METHODS**

In the fluorimetric method of Ciotti and Kaplan,[3502] the oxidized forms of NAD and NADP react with methyl ethyl ketone in 3.5*N* NaOH solution followed by acidification to give a fluorescent product, which is monitored in a fluorimeter at an excitation wavelength of 360 nm and an emission wavelength of 450 nm. NADH and NADPH are destroyed by this treatment. Since this reaction does not distinguish between the dinucleotides, it is necessary to carry out additional assays. NAD and NADP are measured by the *decrease* in fluorescence following incubation of a portion of the extract with alcohol dehydrogenase (reaction 1, Table 6-1) or isocitrate dehydrogenase (reaction 6, Table 6-1).[3454,3456] Conversely, NADH and NADPH are measured by the *increase* in fluorescence following incubation of a portion of the extract with alcohol dehydrogenase (reaction 1, Table 6-1) or glutathione reductase.[3456] To avoid the manipulations required in the Ciotti and Kaplan method, Wigge *et al.*[3413] made use of enzymatic indicator solutions that permit all four of the dinucleotides to be measured directly. Rhodes and Wooltorton[3455] used the indicator resazurin, which is highly fluorescent in its reduced form resorufin, in procedures analogous to those of the spectrophotometric method described in method 7B. Asali *et al.*[3432] described the use of a bioreactor to monitor the fluorescence of NAD(P)H online in *Catharanthus roseus* callus suspension cultures while being subjected *in vivo* to various metabolic perturbations.

**(D) $^{32}$P RADIOACTIVITY METHOD**

A novel method was developed by Cheung and Suhadolnik[3504] in which the [$^{32}$P]-labeled $PP_i$-NAD pyrophosphorylase reaction (reaction 3, Table 6-1) is coupled with the glucose-hexokinase reaction (Chapter 1, Figure 1-5, reaction 14) to convert NAD to β-[$^{32}$P]ADP, which is then selectively adsorbed on activated charcoal and counted by liquid scintillation. This procedure, used to quantitate NAD in crude extracts of germinating wheat embryos, is capable of measuring NAD in amounts as low as 1 pmol.[3504]

## Analysis Without Separation

### *$^{31}$P Nuclear Magnetic Resonance (NMR) Method*

The proton-decoupled $^{31}$P NMR spectra of NAD and NADP in neutral aqueous solutions exhibit overlapping AB quartets for the two pyrophosphate P atoms in the −9 to −12 ppm region (relative to $P_i = 0$) and NADP shows an additional singlet for the 2′-P atom in the +4 ppm region. In contrast, the reduced dinucleotides NADH and NADPH show only singlets for the diphosphate P atoms despite their obviously different chemical environments.[68,3505,3506] Bligny *et al.* found such patterns in the $^{31}$P spectra of perchloric acid extracts of spinach leaves and chloroplasts,[50] sycamore cell suspension cultures[3341] and potato tuber mitochondria,[2708] but assigned the two AB quartets to (NAD + NADP) and (NADH + NADPH). This is inconsistent with the known behavior of the reduced dinucleotides in acid solution discussed earlier. It appears more likely that the downfield AB quartet represents NAD alone and the upfield AB quartet and associated singlet represent NADP alone. The results are so listed in Table 6-2.

The $^{31}$P method has also been applied to living tissues kept under constant aeration as described previously for other phosphorus-containing metabolites. A small peak in the −10 ppm region has been ascribed to NAD in the $^{31}$P NMR spectra of sycamore,[3341] *Rosa damascena*,[2695] carrot,[2507] and Madagascar periwinkle[2507] cell suspension cultures; in pea[526] and corn[544] root tips; and in fiddleneck sprouts,[2644] spinach leaves,[50] Jerusalem artichoke stolons,[45] tobacco pollen grains,[2563] soybean nodules,[2563] and sunflower stems,[2563] but other phosphorus-containing compounds (notably UDPG) also have signals in this region and the resolution is insufficient for positive identification.

## Physical Properties

Nicotine Adenine Dinucleotide (NAD), $C_{21}H_{27}N_7O_{14}P_2$, also called Diphosphopyridine Nucleotide (DPN). *Adenosine 5′-(Trihydrogen Diphosphate), P′ → 5′ Ester with 3-(Aminocarbonyl)-1-β-D-ribofuranosylpyridinium, Inner Salt.*

NAD [R.N. 53-84-9]: Luminescence,[3507] phosphorescence (fig.),[2920] molecular self-association,[3508] molar absorptivity ($\varepsilon$) $17.4 \times 10^3$ L/mol/cm (260 nm, 25 °C),[3509] diamagnetic susceptibility ($\chi_M$) $-342 \times 10^{-6}$ cm$^3$/mol at 25 °C,[3510] dipole moment (D) 250 esu cm,[2939] countercurrent distribution,[3511,3512] heat capacity,[3513] ODMR,[2920] cyclic voltammetry (fig.),[3514] polarography,[3515] NOE.[3516] Ionization constants: p$K_a$ 3.88 (potentiometric, 25 °C),[3517] 12.13, 12.17, 12.75, and 12.78 for the four ribosyl OH groups ($^{13}$C NMR, 20 °C).[3518] Spectra: UV (fig.),[3519] FTIR (fig.),[3520] Raman (fig.),[3521] UV Raman (fig.),[3522] [$^1$H] NMR (fig.),[3523,3524] [$^{13}$C] NMR (fig.),[359] [$^{15}$N] NMR (fig.),[3525] [$^{31}$P] NMR (fig.),[3505] 2d[$^{13}$C-$^{31}$P] NMR (fig.),[2882] ORD (fig.),[2923] CD (fig.),[3526] SERS (fig.),[3527] FAB-MS (fig.),[3528] FD-MS (fig.),[3528] ESI-MS,[2887] LID-MS (fig.).[3529] Chromatography: PC,[3530] TLC,[3531] HPTLC,[2891] IEC,[2894] HPLC,[2440] preparative HPLC,[3532] GC,[3156] GFC,[2893] DEAE cellulose column.[3533] Electrophoresis: PE,[9] CZE,[3534] capillary isotachophoresis,[3239] MECC.[3535] Theoretical calculations: LCAO-MO,[3536,3537]

**Table 6-2** Nicotinamide Adenine Dinucleotides in Plants*

| No. | Plant part | Method | NAD | NADH | NADP | NADPH | References |
|---|---|---|---|---|---|---|---|
| *Abutilon molle* Sweet (Indian Mallow) | | | | | | | |
| 1 | Seed[a] | Fluor. | 11.2[b] | | | | 3420 |
| *Acacia diethriciana* F. Müll. | | | | | | | |
| 1 | Seed[a] | Fluor. | 18.8[b] | | | | 3420 |
| *Acanthus mollis* L. (Bear's Breech) | | | | | | | |
| 1 | Leaf[a] | Fluor. | 34[b] | | | | 3421 |
| *Acer pseudoplatanus* L. (Sycamore Maple) | | | | | | | |
| 1 | Cell suspension culture[c] | IEC | 6 | | | | 2447 |
| 1 | Cell suspension culture[d] | Enzym. | 18 | 5 | 1.9 | 1.0 | 2449 |
| 1 | Cell suspension culture | $^{31}$P NMR | + | | + | | 3341 |
| *Aegilops speltoides* Tausch (Goatgrass) | | | | | | | |
| 1 | Leaf | Enzym. | 14.9 | 1.4 | 28.1 | 10.3 | 3416 |
| *Aegilops squarrosa* L. (Barb Goatgrass) | | | | | | | |
| 1 | Leaf | Enzym. | 7.3 | 3.2 | 3.3 | 25.6 | 3416 |
| *Albizia lophantha* (Willd.) Benth. (Plume Albizzia) | | | | | | | |
| 1 | Seed | Fluor. | 12[e] | | | | 3420 |
| *Allium neapolitanum* Cirillo (White Garlic) | | | | | | | |
| 1 | Seed[a] | Fluor. | 2.8[b] | | | | 3420 |
| *Angelica silvestris* L. (Woodland Angelica) | | | | | | | |
| 1 | Seed[a] | Fluor. | 4.1[b] | | | | 3420 |
| *Aquilegia vulgaris* L. (European Columbine) | | | | | | | |
| 1 | Seed[a] | Fluor. | 2[b] | | | | 3420 |
| *Asplenium nidus* L. (Hawaii Birdnest Fern) | | | | | | | |
| 1 | Adult leaf[c] | Enzym. | 41 | 23 | 28 | 53 | 3422 |
| *Avena sativa* L. (Oats) | | | | | | | |
| 1 | Seed[a] | Fluor. | 5[b] | | | | 3423 |
| 1 | Sprout, embryo | Enzym. | 40.5 | 6.5 | 9.2 | 20.0 | 3424 |
| 1 | –, coleoptile node[f] | Enzym. | 4.0 | 6.0 | 8.9 | 5.2 | 3425 |
| 1 | Leaf, chloroplast[g] | Enzym. | 4.1 | 4.0 | 2.4 | 0.9 | 231 |
| 1 | –, mitochondria[g] | Enzym. | 3.5 | 1.9 | <0.5 | <0.5 | 231 |
| 1 | –, cytosol and vacuole[g] | Enzym. | 12.0 | 1.5 | 1.8 | 6.5 | 231 |
| 1 | Seedling[a] | Fluor. | 2.58[b] | | | | 3423 |
| 1 | Seedling | IEC | 15.6 (incl. CMP) | | | | 2473 |
| 1 | Mature, aerial parts | IEC | | | 12 | | 2471 |
| *Beta vulgaris* L. (Sugar Beet) | | | | | | | |
| 1 | Leaf[h] | Enzym. | 8.87 | 2.23 | 3.28 | 2.24 | 3426 |
| 1 | –, chloroplast[c,i] | Enzym. | 1.1 | | 28 | 7 | 3427 |
| 1 | –, cytoplasm[c,i] | Enzym. | 4.3 | | 0.5 | 3 | 3427 |
| 1 | Root | IEC | 0 | | 8 | | 3345 |
| *Beta vulgaris* L. ssp. *rapacea* (Koch) Döll (Fodder Beet) | | | | | | | |
| 1 | Leaf[c] | Enzym. | | | | 31 | 237 |
| *Betula pubescens* Ehrh. (Downy Birch) | | | | | | | |
| 1 | Pollen[j] | von Euler | 572 | | | | 3428 |

*nmol/g fresh weight basis unless stated otherwise; [a]µg/g; [b]Incl. NADP and NMN; [c]Dry weight basis; [d]nmol/$10^7$ cells; [e]Including NADH; [f]nmol/plant part; [g]nmol/mg chlorophyll; [h]µmol/$m^2$; [i]nmol/mg protein; [j]Relative to brewer's yeast cozymase = 100; [k]pmol/seedling; [l]µmol/mg chlorophyll; [m]Including NADPH; [n]Based on its degradation product, ADPRib 2′ = phosphate; [o]Cozymase units; [p]nmol/$-10^9$ plastids; [q]µmol/mmol chlorophyll; [r]m*M*; [s]µg/seedling; [t]ng/g.

*Continued*

**Table 6-2** Nicotinamide Adenine Dinucleotides in Plants*—cont'd

| No. | Plant part | Method | NAD | NADH | NADP | NADPH | References |
|---|---|---|---|---|---|---|---|
| *Borago officinalis* L. (Common Borage) | | | | | | | |
| 1 | Seed[a] | Fluor. | 4.3[b] | | | | 3420 |
| *Brassica napus* L. ssp. *oleifera* (Winter Rape) | | | | | | | |
| 1 | Leaf | Enzym. | 6 | 2 | 9 | 3 | 3429 |
| *Brassica nigra* (L.) Koch. (Black Mustard) | | | | | | | |
| 1 | Seed[a] | Fluor. | 11.1[b] | | | | 3420 |
| *Brassica oleracea* L. ssp. *italica* Plenck. (Broccoli) | | | | | | | |
| 1 | Stems and florets | HPLC | 35 | | | | 2441 |
| *Bryophyllum tubiflorum* Harv. (Chandelier Plant) | | | | | | | |
| 1 | Phyllodia | TLC/TLC | + | | + | | 3346 |
| *Camellia japonica* L. (Camellia) | | | | | | | |
| 1 | Pollen[j] | Okunuki | 111 | | | | 3430 |
| *Camellia sasanqua* Thunb. (Sasanqua) | | | | | | | |
| 1 | Pollen[j] | Okunuki | 50 | | | | 3430 |
| *Cannabis sativa* L. (Hemp) | | | | | | | |
| 1 | Seed[a] | Fluor. | 6.6[b] | | | | 3420 |
| *Capsicum annuum* L. (Bell Pepper) | | | | | | | |
| 1 | Seed[a] | Fluor. | 3[b] | | | | 3420 |
| 1 | Fruit | HPLC | + | | | | 2441 |
| *Carduus crispus* L. (Curly Plume less Thistle) | | | | | | | |
| 1 | Seed[a] | Fluor. | 2.6[b] | | | | 3420 |
| *Carica papaya* L. (Papaya) | | | | | | | |
| 1 | Seed[a] | Fluor. | 2[b] | | | | 3420 |
| *Carthamus tinctorius* L. (Safflower) | | | | | | | |
| 1 | Seed[a] | Fluor. | 6[b] | | | | 3420 |
| *Castanea sativa* Mill. (Chestnut) | | | | | | | |
| 1 | Seed[a] | Fluor. | 17.8[b] | | | | 3420 |
| *Catharanthus roseus* (L.) G. Don (Madagascar Periwinkle) | | | | | | | |
| 1 | Cell suspension culture | Enzym. | | | 4.4 | | 3431 |
| 1 | Cell suspension culture | Fluor. | | + | | + | 3432 |
| 1 | Cell suspension culture | $^{31}$P NMR | + | | | | 2507 |
| *Chelidonium majus* L. (Celandine) | | | | | | | |
| 1 | Seed[a] | Fluor. | 12[b] | | | | 3420 |
| *Chenopodium rubrum* L. (Red Goosefoot) | | | | | | | |
| 1 | Seedling[k] | Enzym. | 114 | 10 | 19 | 35 | 2508 |
| *Chrysanthemum leucanthemum* L. (Oxeye Daisy) | | | | | | | |
| 1 | Leaf[a] | Fluor. | 29[b] | | | | 3421 |
| *Chrysanthemum segetum* L. (Corn Marigold) | | | | | | | |
| 1 | Seed[a] | Fluor. | 7[b] | | | | 3420 |
| *Cicer arietinum* L. (Chickpea) | | | | | | | |
| 1 | Seed[a] | Fluor. | 23.8[b] | | | | 3420 |
| *Cichorium intybus* L. (Chicory) | | | | | | | |
| 1 | Root[c] | Enzym. | 74 | 36 | 6 | 25 | 3433 |
| *Cistus monspelliensis* L. (Montpelier Cistus) | | | | | | | |
| 1 | Seed[a] | Fluor. | 5.5[b] | | | | 3420 |
| *Citrullus vulgaris* Schrad. (Watermelon) | | | | | | | |
| 1 | Seedling, cotyledon[f] | Enzym. | 7.60 | 0.02 | 0.01 | 1.30 | 3411 |
| 1 | –, hypocotyl[f] | Enzym. | 0.16 | 0.29 | 2.09 | 3.83 | 3411 |

**Table 6-2** Nicotinamide Adenine Dinucleotides in Plants*—cont'd

| No. | Plant part | Method | NAD | NADH | NADP | NADPH | References |
|---|---|---|---|---|---|---|---|
| *Citrus aurantium* L. (Sour Orange) | | | | | | | |
| 1 | Seed[a] | Fluor. | 20[b] | | | | 3420 |
| *Citrus paradisi* Macf. (Grapefruit) | | | | | | | |
| 1 | Mature peeled pulp vesicles | Enzym. | 6.0 | 0.77 | 0.93 | 1.2 | 3434 |
| *Citrus sinensis* (L.) Osbeck (Orange) | | | | | | | |
| 1 | Mature peeled pulp vesicles | Enzym. | 11.8 | 2.5 | 1.2 | 1.6 | 3434 |
| 1 | Juice | IEC | + | | | | 248 |
| *Citrus* spp. (Pineapple Orange) | | | | | | | |
| 1 | Fruit juice vesicles | Enzym. | 3430 | | 2700 | | 3435 |
| *Corylus avellana* L. (European Hazel) | | | | | | | |
| 1 | Seed[a] | Fluor. | 9[b] | | | | 3420 |
| *Costus speciosus* (J. König) Sm. (Crepe Ginger) | | | | | | | |
| 1 | Cell suspension culture | HPLC | 56 | 296 | 22 | 33 | 2523 |
| *Cucumis sativus* L. (Cucumber) | | | | | | | |
| 1 | Leaf | Enzym. | 27.0 | 4.8 | 12.9 | 5.8 | 3436 |
| 1 | –, plastid | Enzym. | NADH/NAD and NADPH/NADP ratios given | | | | 3437 |
| 1 | –, chloroplast[l] | Fluor. | 40.8[b] | | | | 3438 |
| 1 | Seedling, cotyledon | Enzym. | 80.4 | 19.4 | 13.0 | 27.9 | 3439 |
| 1 | –, hypocotyl[l] | Enzym. | 2.4 | 0 | 0.8 | 0 | 3440 |
| 1 | –, cell wall[l] | Enzym. | 5.1 | 0 | 0 | 0 | 3440 |
| 1 | –, mitochondria[i] | Enzym. | 0.5 | | | | 3441 |
| 1 | –, root | Enzym. | 0.323 | 0.438 | | | 3442 |
| *Cucurbita maxima* Duch. (Squash) | | | | | | | |
| 1 | Seedling, cotyledon | Enzym. | 11.6 | 1.62 | 16.8 | 12.4 | 3443 |
| 1 | –, leaf | Enzym. | 36.8 | 4.20 | 32.5 | 11.6 | 3443 |
| *Cucurbita pepo* L. (Pumpkin) | | | | | | | |
| 1 | Leaf[c] | IEC | 2300 | 900 | 1400 | 1900 | 2530 |
| 1 | –, chloroplast[c] | IEC | 150 | 160 | 140 | 140 | 2530 |
| 1 | –, mitochondria[c] | Enzym. | 173 | 176 | 149 | 164 | 1633 |
| 1 | Stem, phloem exudate | IEC | + | | + | | 251 |
| 1 | Fruit, unripe | IEC | + | | + | | 251 |
| 1 | –, ripe | IEC | + | | + | | 251 |
| *Cuscuta reflexa* Roxb. (Dodder) | | | | | | | |
| 1 | Leaf | TLC/TLC | + | | + | | 33 |
| *Datura inoxia* Mill. (Downy Thorn Apple) | | | | | | | |
| 1 | Cell suspension culture | HPLC | 26 | | 7.2 | | 2440 |
| *Daucus carota* L. (Carrot) | | | | | | | |
| 1 | Cell suspension culture | $^{31}$P NMR | + | | | | 2507 |
| *Digitalis lanata* Ehrh. (Grecian Foxglove) | | | | | | | |
| 1 | Leaf[h] | Lumin. | | | | 23.5 | 2540 |
| *Digitalis purpurea* L. (Digitalis) | | | | | | | |
| 1 | Seed[a] | Fluor. | 9.5[b] | | | | 3420 |

*nmol/g fresh weight basis unless stated otherwise; [a]μg/g; [b]Incl. NADP and NMN; [c]Dry weight basis; [d]nmol/$10^7$ cells; [e]Including NADH; [f]nmol/plant part; [g]nmol/mg chlorophyll; [h]μmol/$m^2$; [i]nmol/mg protein; [j]Relative to brewer's yeast cozymase = 100; [k]pmol/seedling; [l]μmol/mg chlorophyll; [m]Including NADPH; [n]Based on its degradation product, ADPRib 2′ = phosphate; [o]Cozymase units; [p]nmol/−$10^9$ plastids; [q]μmol/mmol chlorophyll; [r]m*M*; [s]μg/seedling; [t]ng/g.

*Continued*

**Table 6-2** Nicotinamide Adenine Dinucleotides in Plants*—cont'd

| No. | Plant part | Method | NAD | NADH | NADP | NADPH | References |
|---|---|---|---|---|---|---|---|
| *Diospyros kaki* L.f. (Japanese Persimmon) | | | | | | | |
| 1 | Seed[a] | Fluor. | 5[b] | | | | 3420 |
| *Echinochloa oryzicola* Vasin. (Rice Barnyardgrass) | | | | | | | |
| 1 | Sprout | – | | 0.090[m] | | | 3444 |
| *Egeria densa* Planch. (Brazilian Waterweed) | | | | | | | |
| 1 | Leaf | TLC/TLC | + | | + | | 33 |
| *Elodea canadensis* Michx. (Canadian Waterweed) | | | | | | | |
| 1 | Leaf[a] | Fluor. | 20[b] | | | | 3421 |
| *Escholtzia californica* Cham. (California Poppy) | | | | | | | |
| 1 | Seed[a] | Fluor. | 12.3[b] | | | | 3420 |
| *Euonymus europaeus* L. (European Spindletree) | | | | | | | |
| 1 | Seed[a] | Fluor. | 20[b] | | | | 3420 |
| *Euphorbia lathyris* L. (Caper Spurge) | | | | | | | |
| 1 | Seed[a] | Fluor. | 4[b] | | | | 3420 |
| *Flaveria brownii* A. Powell (Brown's Yellowtops) | | | | | | | |
| 1 | Leaf[c] | Enzym. | 19.1 | 17.7 | 15.7 | 20.8 | 3422 |
| *Flaveria cronquistii* A. Powell (Yellowtops) | | | | | | | |
| 1 | leaf[c] | Enzym. | 39.8 | 27.4 | 36.0 | 39.2 | 3422 |
| *Flaveria pubescens* Rudb. (Yellowtops) | | | | | | | |
| 1 | Leaf[c] | Enzym. | 35.1 | 16.0 | 29.8 | 26.2 | 3422 |
| *Flaveria trinervia* (Spreng) C. Mohr (Clustered Yellowtops) | | | | | | | |
| 1 | Leaf[c] | Enzym. | 84.5 | 55.8 | 67.4 | 70.2 | 3422 |
| *Glycine max* (L.) Merr. (Soybean) | | | | | | | |
| 1 | Seed, immature[c] | IEC | 3900 (incl. CMP) | | | | 2552 |
| 1 | Seed, mature[c] | IEC | 0 | | | | 2552 |
| 1 | Seed | IEC | | | 2.5 | | 2553 |
| 1 | Leaf | Enzym. | 20.5 | 4.8 | 19.6 | 15.4 | 2558 |
| 1 | Leaf[g] | HPLC | | | 18 | 22 | 26 |
| 1 | Root | Enzym. | 7.7 | 7.0 | 1.0 | 21.5 | 2558 |
| 10 | Nodule | Enzym. | 15.8-118 | 7.0-33.1 | 1.9-11.8 | 9.7-26.6 | 3445 |
| 1 | Nodule | HPLC | 143 (incl. UMP) | | 37.1 (incl. UDP) | | 3446 |
| 1 | Nodule | $^{31}$P NMR | + | | | | 2563 |
| 1 | Seedling, cotyledon[f] | Enzym. | 36.90 | 21.20 | 1.80 | 4.03 | 3411 |
| 1 | –, hypocotyl[f] | Enzym. | 0.58 | 0.29 | 1.02 | 1.89 | 3411 |
| *Glycine soja* (L.) Sieb. and Zucc. (Soybean) | | | | | | | |
| 1 | Seed[a] | Fluor. | 70.9[b] | | | | 3420 |
| *Gossypium arboreum* L. (Tree Cotton) | | | | | | | |
| 1 | Seed hair, primary wall[f] | IEC | 62 | | 8 | | 2566 |
| 1 | –, secondary wall[f] | IEC | 87 | | 7 | | 2566 |
| *Gossypium hirsutum* L. (Upland Cotton) | | | | | | | |
| 1 | Leaf[c] | IEC | + | | 70 | 53[n] | 2569 |
| 1 | Root[c] | IEC | + | | 78 | 96[n] | 2569 |
| *Hedera helix* L. (English Ivy) | | | | | | | |
| 1 | Juvenile leaf[c] | Enzym. | 36 | 23 | 47 | 53 | 3422 |
| *Helianthus annuus* L. (Sunflower) | | | | | | | |
| 1 | Leaf | IEC | + | | | | 3355 |
| 1 | Leaf | Enzym. | 24.4 | 2.4 | 6.5 | 18.5 | 2558 |
| 1 | Root | Enzym. | 5.9 | 11.1 | 2.5 | 16.4 | 2558 |

**Table 6-2** Nicotinamide Adenine Dinucleotides in Plants*—cont'd

| No. | Plant part | Method | NAD | NADH | NADP | NADPH | References |
|---|---|---|---|---|---|---|---|
| 1 | Stem | $^{31}$P NMR | + | | | | 2563 |
| 1 | Seedling, cotyledon[f] | Enzym. | 11.10 | 0.79 | 0.70 | 2.58 | 3411 |
| 1 | –, hypocotyl[f] | Enzym. | 0.38 | 0.01 | 2.63 | 9.50 | 3411 |
| *Helianthus tuberosus* L. (Jerusalem Artichoke) | | | | | | | |
| 1 | Tuber | IEC | 0 | | 2 | | 2576 |
| 1 | Young stolon | $^{31}$P NMR | + | | | | 45 |
| *Hordeum vulgare* L. (Barley) | | | | | | | |
| 1 | Seed[a] | Fluor. | 10[b] | | | | 3420 |
| 1 | Leaf | Enzym. | 39 | 2.0 | 12 | 3.0 | 3447 |
| 1 | Leaf | HPLC | 15.2 | | 16.0 | | 2585 |
| 1 | –, protoplast[g] | Enzym. | 20.1[e] | | 24.4[m] | | 3413 |
| 1 | –, chloroplast[g] | Enzym. | 5.2 | 2.1 | 9.8 | 9.7 | 3413 |
| 1 | –, mitochondria[g] | Enzym. | 2.0 | 0.1 | <0.5 | <0.5 | 3413 |
| 1 | –, cytosol[g] | Enzym. | 8.6 | 2.0 | 1.8 | 3.4 | 3413 |
| 1 | Primary leaf[c] | HPLC | 100-200 | | 200-300 | | 3448 |
| 1 | Root[c] | HPLC | ~25 | | ~25 | | 3448 |
| 1 | Root tip[o] | von Euler | 3.5 | | | | 3405 |
| 1 | Mature, aerial parts | IEC | | | 9 | | 2471 |
| *Hyphaenae thebaica* Mart. (Doum Palm) | | | | | | | |
| 1 | Seed[a] | Fluor. | 0.6[b] | | | | 3420 |
| *Isoetes duriei* (Bory) | | | | | | | |
| 1 | Leaf | TLC/TLC | + | | + | | 33 |
| *Juglans regia* L. (English Walnut) | | | | | | | |
| 1 | Seed[a] | Fluor. | 33[b] | | | | 3420 |
| *Kalanchoë daigremontiana* Ham. and Perr. (Devil's Backbone) | | | | | | | |
| 1 | Leaf[c] | Enzym. | 28 | 15 | 67 | 76 | 3422 |
| *Lactuca sativa* L. (Lettuce) | | | | | | | |
| 1 | Sprout | HPLC | + | | | | 2598 |
| *Larix decidua* Mill. (European Larch) | | | | | | | |
| 1 | Primary wall (cambium) | IEC | 0 | | 0 | | 2601 |
| 1 | Secondary wall (xylem) | IEC | 0.2 | | 0.04 | | 2601 |
| *Leleba oldhami* (Summer Bamboo) | | | | | | | |
| 1 | Desheathed shoot | IEC | | | 2.5 | | 2661 |
| *Lemna gibba* L. (Gibbous Duckweed) | | | | | | | |
| 1 | Whole plant | TLC/TLC | + | | + | | 33 |
| 1 | Whole plant | Enzym. | 17.5 | 1.4 | 2.0 | 3.4 | 3449 |
| | | and diurnal variation | | | | | 3449 |
| *Lemna paucicostata* Hegelm. (Lesser Duckweed) | | | | | | | |
| 1 | Frond, at floral induction[a] | Enzym. | 31.7 | | | | 3450 |
| *Lens culinaris* Medik. (Lentil) | | | | | | | |
| 1 | Seed[a] | Fluor. | 43[b] | | | | 3420 |

*nmol/g fresh weight basis unless stated otherwise; [a]μg/g; [b]Incl. NADP and NMN; [c]Dry weight basis; [d]nmol/$10^7$ cells; [e]Including NADH; [f]nmol/plant part; [g]nmol/mg chlorophyll; [h]μmol/$m^2$; [i]nmol/mg protein; [j]Relative to brewer's yeast cozymase = 100; [k]pmol/seedling; [l]μmol/mg chlorophyll; [m]Including NADPH; [n]Based on its degradation product, ADPRib 2′ = phosphate; [o]Cozymase units; [p]nmol/−$10^9$ plastids; [q]μmol/mmol chlorophyll; [r]m*M*; [s]μg/seedling; [t]ng/g.

*Continued*

**Table 6-2** Nicotinamide Adenine Dinucleotides in Plants*—cont'd

| No. | Plant part | Method | NAD | NADH | NADP | NADPH | References |
|---|---|---|---|---|---|---|---|
| *Lilium auratum* Lindl. (Golden-Rayed Lily) | | | | | | | |
| 1 | Pollen[j] | Okunuki | 118 | | | | 3430 |
| *Lilium longiflorum* Thunb. (Trumpet Lily) | | | | | | | |
| 1 | Pollen[j] | Okunuki | 109 | | | | 3430 |
| *Lilium philippinense* Bak. (Philippine Lily) | | | | | | | |
| 1 | Pollen[j] | Okunuki | 103 | | | | 3430 |
| *Luffa aegyptiaca* Mill. (Sponge Gourd) | | | | | | | |
| 1 | Seed[a] | Fluor. | 12.2 | | | | 3420 |
| *Lupinus albus* L. (White Lupine) | | | | | | | |
| 1 | Seed[a] | Fluor. | 27[b] | | | | 3420 |
| *Lupinus luteus* L. (Yellow Lupine) | | | | | | | |
| 1 | Seed | IEC | + | +[n] | + | +[n] | 2437 |
| 1 | Root cortex | Enzym. | 18.8 | 21.4 | 5.5 | 11 | 3451 |
| 1 | Whole nodule | Enzym. | 66 | 68 | 16 | 46 | 3451 |
| 1 | Nodule cortex | Enzym. | 47 | 47 | 18 | 24 | 3451 |
| *Lycopersicon esculentum* Mill. (Tomato) | | | | | | | |
| 1 | Leaf | Fluor. | | + | | | 3452 |
| 1 | Leaf[c] | IEC | 122 | 16[n] | 137 | 48[n] | 3453 |
| 1 | Leaf | Enzym. | 32.7 | | 29.3 | | 3454 |
| 1 | Stem | Fluor. | | + | | | 3452 |
| 1 | Seedling, root | Enzym. | 0.057 | 0.320 | | | 3442 |
| *Magnolia grandiflora* L. (Southern Magnolia) | | | | | | | |
| 1 | Leaf | IEC | + | | + | | 2543 |
| *Malus domestica* Borkh. (Apple) | | | | | | | |
| 1 | Fruit, peel | Enzym. | 22.2 | 2.1 | 2.2 | 6.1 | 3455 |
| 1 | –, pulp | Enzym. | 10.0 | 1.0 | 1.0 | 1.1 | 3455 |
| *Malva rotundifolia* L. (Dwarf Mallow) | | | | | | | |
| 1 | Seed[a] | Fluor. | 7.7[b] | | | | 3420 |
| *Matthiola incana* (L.) R.Br. (Tenweeks Stock) | | | | | | | |
| 1 | Leaf[p] | Fluor. | 35[b] | | | | 3421 |
| *Medicago sativa* L. (Alfalfa) | | | | | | | |
| 1 | Seed[a] | Fluor. | 11.9[b] | | | | 3420 |
| 2 | Root nodule (1) | Enzym. | 58.2 | 37.1 | 2.2 | 7.5 | 3445 |
| | Root nodule (2) | | 17.9 | 16.1 | 0.7 | 4.9 | 3445 |
| *Melianthus majus* L. (Honey Flower) | | | | | | | |
| 1 | Seed[a] | Fluor. | 18.8[b] | | | | 3420 |
| *Milium multiflorum* Cav. (Millet Grass) | | | | | | | |
| 1 | Seed[a] | Fluor. | 3.1[b] | | | | 3420 |
| *Mimosa pudica* L. (Shameplant) | | | | | | | |
| 1 | Seed[a] | Fluor. | 6[b] | | | | 3420 |
| *Mirabilis jalapa* L. (Marvel of Peru) | | | | | | | |
| 1 | Seed[a] | Fluor. | 10[b] | | | | 3420 |
| *Molinia coerulea* (L.) Moench. (Purple Moorgrass) | | | | | | | |
| 1 | Seed[a] | Fluor. | 1.6[b] | | | | 3420 |
| *Momordica charantia* L. (Balsam Pear) | | | | | | | |
| 1 | Seed[a] | Fluor. | 5.5[b] | | | | 3420 |
| *Muscari comosum* (L.) Mill. (Tassel Grape Hyacinth) | | | | | | | |
| 1 | Seed[a] | Fluor. | 7[b] | | | | 3420 |

**Table 6-2** Nicotinamide Adenine Dinucleotides in Plants*—cont'd

| No. | Plant part | Method | NAD | NADH | NADP | NADPH | References |
|---|---|---|---|---|---|---|---|
| *Nelumbo nucifera* Gaertn. (Sacred Lotus) | | | | | | | |
| 1 | Seed[a] | Fluor. | 12.7[b] | | | | 3420 |
| *Nicotiana glutinosa* L. (Tobacco) | | | | | | | |
| 1 | Leaf[a] | Enzym. | 5.5 | 0.8 | 3.0 | 0.2 | 3409 |
| *Nicotiana longiflora* Cav. (Longflower Tobacco) | | | | | | | |
| 1 | Leaf[a] | Fluor. | 28[b] | | | | 3421 |
| *Nicotiana tabacum* L. (Tobacco) | | | | | | | |
| 1 | Seed[a] | Fluor. | 5.6[b] | | | | 3420 |
| 1 | Leaf | HPLC | 22.0 | | 15.2 | | 2440 |
| 1 | Root | HPLC | 2.7 | | 0.7 | | 2440 |
| 1 | Seedling, young leaf[f] | Enzym. | 0.38 | 0 | 3.96 | 1.12 | 3411 |
| 1 | –, old leaf[f] | Enzym. | 11.46 | 0 | 49.5 | 3.84 | 3411 |
| 1 | Seedling, young leaf[f] | HPLC | 30 | | 33 | | 3363 |
| 1 | –, old leaf[f] | HPLC | 10 | | 12 | | 3363 |
| 1 | –, terminal bud[f] | HPLC | 13 | | 10 | | 3363 |
| 1 | Apex | HPLC | 15.7 | | 10.4 | | 2628 |
| 1 | Callus culture[d] | Enzym. | 38 | 9 | 16 | 5 | 3410 |
| 1 | Cell suspension culture | HPLC | 17.6 | | 6.3 | | 2440 |
| 1 | Pollen grain | $^{31}$P NMR | + | | | | 2563 |
| *Ophioglossum lusitanicum* L. (Least Adderstongue) | | | | | | | |
| 1 | Leaf | TLC/TLC | + | | + | | 33 |
| *Ophioglossum vulgatum* L. (Southern Adderstongue) | | | | | | | |
| 1 | Leaf | TLC/TLC | + | | + | | 33 |
| *Oryza sativa* L. (Rice) | | | | | | | |
| 1 | Grain, 10 daf | IEC | 42 | | ~18 | | 2635 |
| 1 | Ripening kernel | IEC | | | 1.6 | | 2540 |
| 1 | Seedling | Enzym. | 4600 | 500 | 3000 | 8500 | 3456 |
| 1 | –, endosperm[f] | Enzym. | 1.48 | 0.16 | 0.15 | 0 | 3411 |
| 1 | –, coleoptile[f] | Enzym. | 0.04 | 0.02 | 0.13 | 0.28 | 3411 |
| *Paeonia albiflora* Pall. (Chinese Peony) | | | | | | | |
| 1 | Pollen[q] | Okunuki | 95 | | | | 3430 |
| *Papaver orientale* L. (Oriental Poppy) | | | | | | | |
| 1 | Pollen[j] | Okunuki | 63 | | | | 3430 |
| *Papaver somniferum* L. (Poppy) | | | | | | | |
| 1 | Pollen[j] | Okunuki | 130 | | | | 3430 |
| *Persea americana* Mill. (Avocado) | | | | | | | |
| 1 | Mature fruit[r] | Enzym. | 0.064 | 0.002 | | | 3457 |
| *Petroselinum crispum* (Mill.) Nym. (Parsley) | | | | | | | |
| 1 | Leaf[a] | Enzym. | 8.6 | | 9.1 | | 3458 |
| *Peumus boldus* Molina (Boldo) | | | | | | | |
| 1 | Seed[a] | Fluor. | 2.4[b] | | | | 3420 |
| *Phacelia tanacetifolia* Benth. (Fiddleneck) | | | | | | | |
| 1 | Seed | $^{31}$P NMR | + | | | | 2644 |

*nmol/g fresh weight basis unless stated otherwise; [a]μg/g; [b]Incl. NADP and NMN; [c]Dry weight basis; [d]nmol/$10^7$ cells; [e]Including NADH; [f]nmol/plant part; [g]nmol/mg chlorophyll; [h]μmol/$m^2$; [i]nmol/mg protein; [j]Relative to brewer's yeast cozymase = 100; [k]pmol/seedling; [l]μmol/mg chlorophyll; [m]Including NADPH; [n]Based on its degradation product, ADPRib 2′ = phosphate; [o]Cozymase units; [p]nmol/−$10^9$ plastids; [q]μmol/mmol chlorophyll; [r]m*M*; [s]μg/seedling; [t]ng/g.

*Continued*

**Table 6-2** Nicotinamide Adenine Dinucleotides in Plants*—cont'd

| No. | Plant part | Method | NAD | NADH | NADP | NADPH | References |
|---|---|---|---|---|---|---|---|
| *Pharbitis nil* Choisy (Morning Glory) | | | | | | | |
| 1 | Seedling, cotyledon[f] | Enzym. | | | 2.0 | 1.2 | 3459 |
| *Phaseolus coccineus* L. (Scarlet Runner Bean) | | | | | | | |
| 1 | Etiolated leaf[f] | Enzym. | 1.00 | 0.20 | 0.94 | 0.82 | 3460 |
| *Phaseolus vulgaris* L. (Beans) | | | | | | | |
| 1 | Seed[a] | Fluor. | 53[b] | | | | 3423 |
| 1 | Leaf | Enzym. | 15.9 | 7.4 | 28.0 | 14.2 | 3461 |
| 1 | Leaf[f] | IEC | <0.2 | <0.2[n] | 0.9 | 0.7[n] | 2650 |
| 1 | –, petiole | IEC | – | | – | 2[n] | 2653 |
| 1 | –, laminae | IEC | 8 | | 1.8 | 7[n] | 2653 |
| 1 | Leaf, young | HPLC | 73 | | 54 | | 2652 |
| 1 | –, mature | HPLC | 40 | | 56 | | 2652 |
| 1 | –, mature | IEC | 11.4 | 8.3[n] | | | 2649 |
| 1 | Leaf, midribs removed[a] | Enzym. | 13.7 | | 9.7 | | 3458 |
| 1 | Whole leaf[q] | Enzym. | 38 | 1 | 11 | 5 | 3462 |
| 1 | –, chloroplast[q] | Enzym. | 26 | 1 | 9 | 4 | 3462 |
| 1 | Root | Enzym. | 9.1 | 5.4 | 17.6 | 6.0 | 3461 |
| 1 | Lateral root | Enzym. | 19 | 1 | 11 | 12 | 3463 |
| 1 | Seedling[s] | Fluor. | 63.40[b] | | | | 3423 |
| 1 | Seedling | Cyanide | 11.5 | | 5.5 | | 2656 |
| *Phaseolus vulgaris* L. ssp. *napus* (Dwarf Kidney Bean) | | | | | | | |
| 1 | Seed | IEC | + | +[n] | + | +[n] | 2437 |
| *Phlomis fruticosa* L. (Shrubby Jerusalem Sage) | | | | | | | |
| 1 | Seed[a] | Fluor. | 8[b] | | | | 3420 |
| *Phoenix dactylifera* L. (Date Palm) | | | | | | | |
| 1 | Seed[a] | Fluor. | 3.1[b] | | | | 3420 |
| *Phyllocactus* spp. | | | | | | | |
| 1 | Pollen[a] | von Euler | 685 | | | | 3428 |
| *Phyllostachys pubescens* [Mazel ex] Houz. (Moso Bamboo) | | | | | | | |
| 1 | Desheathed shoot | IEC | | | 0 | | 2661 |
| *Picea abies* (L.) Karst. (Norway Spruce) | | | | | | | |
| 1 | Needle (leaf)[c] | Enzym. | 135 | 48 | 82 | 42 | 2663 |
| *Pinus densiflora* Sieb. and Zucc. (Japanese Red Pine) | | | | | | | |
| 1 | Pollen[j] | Okunuki | 52 | | | | 3430 |
| *Pinus mugo* Turra (Mugo Pine) | | | | | | | |
| 1 | Pollen[a] | von Euler | 302 | | | | 3428 |
| *Pinus sylvestris* L. (Scotch Pine) | | | | | | | |
| 1 | Seedling (1 year old), root | Enzym. | 58.1 | 24.9 | 9.5 | 22.2 | 3464 |
| 1 | Pollen | Enzym. | 9.6[b] | 9.2[m] | | | 3465 |
| 1 | Pollen[a] | von Euler | 299 | | | | 3428 |
| *Pisum sativum* L. (Peas) | | | | | | | |
| 1 | Seed[a] | Fluor. | 96[b] | | | | 3423 |
| 1 | Seed | Enzym. | 135 | | | | 296 |
| 1 | Seed | IEC | 123 | | | | 24 |
| 1 | Seed | HPLC | 73 | | | | 2441 |
| 1 | Seed[o] | von Euler | 6.0 | | | | 3466 |
| 1 | Mature seed | Cyanide | 1 | | 3 | | 2437 |
| 1 | Mature seed | IEC | | 40[n] | | 14[n] | 2437 |

**Table 6-2** Nicotinamide Adenine Dinucleotides in Plants*—cont'd

| No. | Plant part | Method | NAD | NADH | NADP | NADPH | References |
|---|---|---|---|---|---|---|---|
| 1 | Leaf[a] | Enzym. | 11.7 | 1.9 | 7.0 | 0.7 | 3467 |
| 1 | Leaf′ | Enzym. | 46.3 | 5.0 | 38.9 | 24.1 | 3455 |
| 1 | –, chloroplast[q] | Enzym. | 2.52 | 0.75 | 1.23 | 0.41 | 3468 |
| 1 | Leaf and stem[a] | Enzym. | 8.5 | | 7.5 | | 3458 |
| 1 | Root[c] | Enzym. | 18 | 8 | 3 | 16 | 2683 |
| 1 | Root tip | Enzym. | 45.70 | 1.97 | 3.16 | 10.60 | 3469 |
| 1 | Root tip | $^{31}$P NMR | + | | | | 526 |
| 1 | Root nodule | Enzym. | 53 | 17 | 7.0 | 4.5 | 3470 |
| 1 | Sprout | Cyanide | 2 | | 8 | | 3471 |
| 1 | Sprout | IEC | | 25[n] | | 16[n] | 3471 |
| 1 | Seedling[c] | Enzym. | 399.6 | 38.4 | 130.8 | 20.4 | 3472 |
| 1 | Seedling[s] | Fluor. | 27.20[b] | | | | 3423 |
| 1 | –, internode[a] | Enzym. | | | 8.1 | 6.4 | 3407 |
| *Plantago lanceolata* L. (Narrowleaf Plantain) | | | | | | | |
| 1 | Root | Enzym. | 4.09 | 1.29 | 4.81 | 4.22 | 3473 |
| *Platycerium alcicorne* (Willem.) (Tardieu) | | | | | | | |
| 1 | Adult leaf[c] | Enzym. | 13 | 5 | 7 | 11.5 | 3422 |
| *Polytrichum commune* L. | | | | | | | |
| 1 | Gametophyte without rhizoides[c] | Enzym. | 18 | 13 | 27 | 34 | 3422 |
| *Populus deltoides* × *Populus* cv. *caudina* | | | | | | | |
| 1 | Leaf[g] | Enzym. | 9.7 | 14.4 | 3.7 | 4.5 | 3474 |
| *Populus nigra* L. (Black Poplar) | | | | | | | |
| 1 | Pollen[a] | von Euler | 698 | | | | 3428 |
| *Populus tremula* L. (European Aspen) | | | | | | | |
| 1 | Pollen[a] | von Euler | 688 | | | | 3428 |
| *Prunus armeniaca* L. (Apricot) | | | | | | | |
| 1 | Seed[a] | Fluor. | 23[b] | | | | 3420 |
| *Prunus cerasus* L. (Morello Cherry) | | | | | | | |
| 1 | Seed[a] | Fluor. | 18[b] | | | | 3420 |
| *Prunus dulcis* Webb (Almond) | | | | | | | |
| 1 | Seed[a] | Fluor. | 7.7[b] | | | | 3420 |
| *Prunus persica* (L.) Batsch (Peach) | | | | | | | |
| 1 | Seed[a] | Fluor. | 17[b] | | | | 3420 |
| *Pyrus communis* L. (Pear) | | | | | | | |
| 1 | Fruit, peel | Enzym. | 43.4 | 7.4 | 5.0 | 13.0 | 3455 |
| 1 | –, pulp | Enzym. | 12.0 | 1.5 | 4.1 | 6.1 | 3455 |
| *Pyrus serotina* (Japanese Pear) | | | | | | | |
| 1 | Fruit, flesh[t] | Enzym. | 5.9 | 2.2 | 1.2 | <0.1 | 3475 |
| *Raphanus sativus* L. (Radish) | | | | | | | |
| 1 | Leaf | Enzym. | 7.2 | 2.1 | 3.8 | 1.5 | 3419 |
| 1 | Globe root | Enzym. | 2.5 | 2.0 | 0.9 | 1.0 | 3419 |
| *Reseda lutea* L. (Yellow Mignonette) | | | | | | | |
| 1 | Seed[a] | Fluor. | 1[b] | | | | 3420 |

*nmol/g fresh weight basis unless stated otherwise; [a]μg/g; [b]Incl. NADP and NMN; [c]Dry weight basis; [d]nmol/$10^7$ cells; [e]Including NADH; [f]nmol/plant part; [g]nmol/mg chlorophyll; [h]μmol/$m^2$; [i]nmol/mg protein; [j]Relative to brewer's yeast cozymase = 100; [k]pmol/seedling; [l]μmol/mg chlorophyll; [m]Including NADPH; [n]Based on its degradation product, ADPRib 2′ = phosphate; [o]Cozymase units; [p]nmol/−$10^9$ plastids; [q]μmol/mmol chlorophyll; [r]m*M*; [s]μg/seedling; [t]ng/g.

*Continued*

**Table 6-2** Nicotinamide Adenine Dinucleotides in Plants*—cont'd

| No. | Plant part | Method | NAD | NADH | NADP | NADPH | References |
|---|---|---|---|---|---|---|---|
| *Ricinus communis* L. (Castor Bean) | | | | | | | |
| 1 | Seed | HPLC | + | | 0 | | 3476 |
| 1 | Seedling, endosperm[f] | Enzym. | 25.30 | 14.75 | 8.57 | 4.73 | 3411 |
| 1 | –, hypocotyl.[f] | Enzym | 2.24 | 0.01 | 0.05 | 8.24 | 3411 |
| 1 | –, cytosol[i] | Enzym. | 0.33[e] | | 47.6[m] | | 3477 |
| 1 | –, mitochondria[i] | Enzym. | 4.05 | 0 | 46.9 | 0 | 3477 |
| 1 | –, glyoxysome[i] | Enzym. | 0.48 | 0.12 | 3.5[m] | | 3477 |
| 1 | –, plastid[i] | Enzym. | 0.41[e] | | 2.0 | 0 | 3477 |
| *Robinia pseudoacacia* L. (Black Locust) | | | | | | | |
| 1 | Seed[a] | Fluor. | 20[b] | | | | 3420 |
| *Rosa damascena* (Damask Rose) | | | | | | | |
| 1 | Cell suspension culture | $^{31}$P NMR | + | | | | 2695 |
| *Saccharum officinarum* L. (Sugar Cane) | | | | | | | |
| 1 | Leaf[c] | Enzym. | 20 | 13 | 51 | 50 | 3422 |
| *Salix alba* L. (White Willow) | | | | | | | |
| 1 | Pollen[a] | von Euler | 730 | | | | 3428 |
| *Salix cinerea* L. (Large Gray Willow) | | | | | | | |
| 1 | Pollen[a] | von Euler | 740 | | | | 3428 |
| *Salix fragilis* L. (Crack Willow) | | | | | | | |
| 1 | Pollen[a] | von Euler | 718 | | | | 3428 |
| *Salix nigricans* Sm. (Dark-Leaved Willow) | | | | | | | |
| 1 | Pollen[a] | von Euler | 1023 | | | | 3428 |
| *Salix viminalis* L. (Basket Willow) | | | | | | | |
| 1 | Pollen[a] | von Euler | 722 | | | | 3428 |
| *Scilla hispanica* Mill. (Spanish Bluebell) | | | | | | | |
| 1 | Seed[a] | Fluor. | 6.5[b] | | | | 3420 |
| *Scirpus holoschoenus* L. (Roundhead Bulrush) | | | | | | | |
| 1 | Seed[a] | Fluor. | 6.3[b] | | | | 3420 |
| *Secale cereale* L. (Rye) | | | | | | | |
| 1 | Seed[a] | Fluor. | 5[b] | | | | 3420 |
| 1 | Leaf | HPLC | 28.6 | | 61.3 | | 2585 |
| *Selaginella denticulata* (L.) Link. (Tooth-Leaved Clubmoss) | | | | | | | |
| 1 | Leaf | TLC/TLC | + | | + | | 33 |
| *Sesamum indicum* L. (Sesame) | | | | | | | |
| 1 | Seed[a] | Fluor. | 52.3[b] | | | | 3420 |
| *Setaria verticillata* (L.) Beauv. (Bristly Foxtail) | | | | | | | |
| 1 | Seed[a] | Fluor. | 3.7[b] | | | | 3420 |
| *Sinapis alba* L. (White Mustard) | | | | | | | |
| 1 | Leaf | TLC/TLC | + | | + | | 33 |
| 1 | Sprout, cotyledon[c,k] | Enzym. | 500 | 35 | 40 | 170 | 3478 |
| 1 | –, hypocotyl[c,k] | Enzym. | | 23 | | 68 | 3478 |
| 1 | –, root[c,k] | Enzym. | | 10 | | 51 | 3478 |
| *Solanum tuberosum* L. (Potato) | | | | | | | |
| 1 | Tuber | PC/PC | + | + | + | | 9 |
| 1 | Tuber | PC/PE | + | + | + | | 9 |
| 1 | Tuber | Enzym. | 7.2 | 1.2 | 0.4 | 1.1 | 3479 |
| 1 | Tuber, mitochondria | Enzym. | 0.68 | 0.06 | 0.11 | 0.02 | 3479 |
| 1 | –, mitochondria[i] | $^{31}$P NMR | 0.25 | | 0.72 | | 2708 |
| 1 | –, starch grain | IEC | + | | | | 3480 |

**Table 6-2** Nicotinamide Adenine Dinucleotides in Plants*—cont'd

| No. | Plant part | Method | NAD | NADH | NADP | NADPH | References |
|---|---|---|---|---|---|---|---|
| 1 | Tuber explant | Enzym. | 12 | | 7 | | 3481 |
| 1 | Cell suspension culture[c] | Enzym. | 570 | 100 | 110 | 120 | 3482 |
| *Sorghum bicolor* (L.) Moench. (Sorghum) | | | | | | | |
| 1 | Seed[a] | Fluor. | 2[b] | | | | 3420 |
| *Spinacia oleracea* L. (Spinach) | | | | | | | |
| 1 | Leaf, midribs removed[a] | Enzym. | 13.2 | | 8.6 | | 3458 |
| 1 | Leaf, stroma[g] | Enzym. | 4.8 | 0 | 14.8 | 7.2 | 3483 |
| 1 | –, cytosol and mitochondria[g] | Enzym. | 3.0 | 0 | 0.9 | 12.0 | 3483 |
| 1 | Whole leaf[q] | Enzym. | 30 | 1 | 10 | 17 | 3462 |
| 1 | –, chloroplast[q] | Enzym. | 14 | 0 | 12 | 8 | 3462 |
| 1 | –, chloroplast[g] | HPLC | 3.7 | | + | | 3484 |
| 1 | Leaf | $^{31}$P NMR | + | | | 766 | |
| 1 | –, chloroplast | $^{31}$P NMR | + | | + | | 50 |
| *Spirodela polyrrhiza* (L.) Schleid. (Giant Duckweed) | | | | | | | |
| 1 | Frond[c] | Enzym. | 325 | 59 | 585 | 197 | 3485 |
| 1 | Plastid[c,p] | Enzym. | 40 | 1 | 97 | 17 | 3485 |
| *Stachys officinalis* (L.) Trev. (Common Hedgenettle) | | | | | | | |
| 1 | Seed[a] | Fluor. | 5[b] | | | | 3420 |
| *Stellaria media* (L.) Vill. (Chickweed) | | | | | | | |
| 1 | Leaf | Enzym. | Trace | | 2.7 | | 3406 |
| *Strophanthus hispidus* D.C. | | | | | | | |
| 1 | Seed[a] | Fluor. | 11[b] | | | | 3420 |
| *Thea sinensis* L. (Tea) | | | | | | | |
| 1 | Pollen[j] | Okunuki | 92 | | | | 3430 |
| *Tillandsia usneoides* (L.) L. (Spanish Moss) | | | | | | | |
| 1 | Whole plant | TLC/TLC | + | | + | | 33 |
| 1 | Whole plant[c] | Enzym. | 7 | 5 | 6 | 11 | 3422 |
| *Trifolium pratense* L. (Red Clover) | | | | | | | |
| 1 | Seed[a] | Fluor. | 7.7[b] | | | | 3420 |
| *Trigonella foenum-graecum* L. (Fenugreek) | | | | | | | |
| 1 | Seed | IEC | + | | | | 2716 |
| *Triticum aestivum* L. (Wheat) | | | | | | | |
| 1 | Seed[a] | Fluor. | 6[b] | | | | 3423 |
| 1 | Seed, embryo | Enzym. | 16.3 | 9.8 | 0 | 0 | 3486 |
| 1 | Seed, embryo | HPLC | + | | | | 2598 |
| 1 | Whole grain | PC/PE | 40 | | | | 2723 |
| 1 | –, endosperm | PC/PE | 50 | | | | 2723 |
| 1 | –, testa and pericarp | PC/PE | 11 | | | | 2723 |
| 1 | Ripening kernel | IEC | | | 2.7 | | 2540 |
| 1 | Leaf | Enzym. | 10.5 | 1.9 | 3.8 | 5.6 | 3416 |
| 1 | Leaf | HPLC | 20.3 | | 15.2 | | 2585 |
| 1 | Leaf[a] | Cyanide | 27[b] | | | | 3487 |
| 1 | Leaf | Lumin. | | 1.55 | | 0.27 | 3488 |

*nmol/g fresh weight basis unless stated otherwise; [a]μg/g; [b]Incl. NADP and NMN; [c]Dry weight basis; [d]nmol/$10^7$ cells; [e]Including NADH; [f]nmol/plant part; [g]nmol/mg chlorophyll; [h]μmol/$m^2$; [i]nmol/mg protein; [j]Relative to brewer's yeast cozymase = 100; [k]pmol/seedling; [l]μmol/mg chlorophyll; [m]Including NADPH; [n]Based on its degradation product, ADPRib 2′ = phosphate; [o]Cozymase units; [p]nmol/$-10^9$ plastids; [q]μmol/mmol chlorophyll; [r]m*M*; [s]μg/seedling; [t]ng/g.

*Continued*

**Table 6-2** Nicotinamide Adenine Dinucleotides in Plants*—cont'd

| No. | Plant part | Method | NAD | NADH | NADP | NADPH | References |
|---|---|---|---|---|---|---|---|
| 1 | Flag leaf[c] | HPLC | 210 | | 290 | | 3374 |
| 1 | Leaf, plastid[p] | Enzym. | 13 | 1.5 | 16 | 11 | 3485 |
| 1 | Leaf, protoplast[c,g] | Enzym. | 23 | 2 | 16 | 3 | 3472 |
| 1 | –, chloroplast[c,g] | Enzym. | 13 | 7 | 2 | 0.5 | 3472 |
| 1 | Seedling[s] | Fluor. | 2.92[b] | | | | 3423 |
| 1 | Seedling | Enzym. | 6000 | 2500 | 16,000 | 39,500 | 3456 |
| 1 | Seedling, endosperm[f] | Enzym. | 1.88 | 0.04 | 0.44 | 0.06 | 3411 |
| 1 | –, coleoptile[f] | Enzym. | 0.10 | 0.05 | 0.74 | 0.91 | 3411 |
| 1 | –, shoot[c] | Enzym. | 78.3 | 33.1 | 86.5 | 75.7 | 3422 |
| 1 | –, root tip | Enzym. | 7.45 | 3.73 | 1.24 | 1.38 | 3489 |
| *Triticum boeoticum* Boiss. (Wild Einkorn) | | | | | | | |
| 1 | Leaf | Enzym. | 14.3 | 5.1 | 50.3 | 25.0 | 3416 |
| *Triticum compactum* Host (Club Wheat) | | | | | | | |
| 1 | Leaf[a] | Cyanide | 31.0[b] | | | | 3487 |
| *Triticum dicoccoides* ([Körn. ex] Asch. and Grabner) Aarons (Wild Emmer) | | | | | | | |
| 1 | Leaf | Enzym. | 12.9 | 4.5 | 10.6 | 13.1 | 3416 |
| *Triticum dicoccum* Schrank. (Emmer) | | | | | | | |
| 1 | Leaf | Enzym. | 10.1 | 4.9 | 17.6 | 18.7 | 3416 |
| 1 | –, chloroplast[c] | Enzym. | 399 | 22.7 | 113 | 17.6 | 3490 |
| *Triticum durum* Desf. (Durum Wheat) | | | | | | | |
| 1 | Leaf | Enzym. | 8.6 | 4.6 | 32.8 | 34.4 | 3416 |
| *Triticum monococcum* L. (Einkorn) | | | | | | | |
| 1 | Leaf | Enzym. | 23.1 | 7.0 | 21.4 | 27.4 | 3416 |
| *Triticum spelta* L. (Spelt) | | | | | | | |
| 1 | Leaf | Enzym. | 5.3 | 3.7 | 9.6 | 12.8 | 3416 |
| *Verbascum thapsus* L. (Mullein) | | | | | | | |
| 1 | Seed[a] | Fluor. | 3[b] | | | | 3420 |
| *Vicia faba* L. (Faba Bean) | | | | | | | |
| 1 | Seed | IEC | 2.0 | | | | 2738 |
| 1 | Pod | IEC | 4.7 | | | | 2738 |
| 1 | Leaf | TLC/TLC | + | | + | | 33 |
| 1 | Guard cell protoplast[f] | Enzym. | 0.540 | 0.071 | 0.058 | 0.220 | 3491 |
| 1 | Whole seedling | IEC | 4.0 | | | | 2738 |
| *Vicia sativa* L. (Spring Vetch) | | | | | | | |
| 1 | Seed[a] | Fluor. | 13.3[b] | | | | 3420 |
| *Vigna angularis* (Willd.) Ohwi and Ohashi (Adzuki Bean) | | | | | | | |
| 1 | Seedling, cotyledon[f] | Enzym. | 34.70 | 6.56 | 4.99 | 1.89 | 3411 |
| 1 | –, epicotyl[f] | Enzym. | 3.00 | 2.81 | 4.66 | 5.77 | 3411 |
| *Vigna radiata* (L.) Wilcz. (Mung Bean) | | | | | | | |
| 1 | Sprout | IEC | + | | + | | 2742 |
| 1 | –, hypocotyl | IEC | | | 29 | | 2744 |
| 1 | Seedling[c] | IEC | 428 | | | | 2433 |
| 1 | Seedling | HPLC | 32 | | | | 2441 |
| 1 | Seedling, leaf | Enzym. | 49.0 | 1.4 | 9.7 | 4.1 | 3492 |
| *Vigna sesquipedalis* (L.) Fruh. (Yard-Long Bean) | | | | | | | |
| 1 | Seedling, cotyledon[f] | Enzym. | 3.86 | 0 | 0.29 | 0.27 | 3411 |
| 1 | –, hypocotyl[f] | Enzym. | 7.20 | 0 | 26.80 | 2.12 | 3411 |
| 1 | –, root tip[f] | Enzym. | 0.064 | 0.034 | 0.122 | 0.085 | 3411 |
| | | and variation from root base to tip | | | | | 3411 |

**Table 6-2** Nicotinamide Adenine Dinucleotides in Plants*—cont'd

| No. | Plant part | Method | NAD | NADH | NADP | NADPH | References |
|---|---|---|---|---|---|---|---|
| *Vigna unguiculata* (L.) Walp. (Cowpea) | | | | | | | |
| 1 | Seed[a] | Fluor. | 46.6[b] | | | | 3420 |
| 1 | Sprout, root mitochondria[i] | Enzym. | 7.2 | | | | 3493 |
| *Wolffia arrhiza* (L.) Wimm. (Spotless Water Meal) | | | | | | | |
| 1 | Whole plant[c] | Enzym. | 225 | 92.7 | 474 | 427 | 3422 |
| *Yucca aloifolia* L. (Aloe Yucca) | | | | | | | |
| 1 | Seed[a] | Fluor. | 2[b] | | | | 3420 |
| *Zea mays* L. (Corn) | | | | | | | |
| 1 | Seed[a] | Fluor. | 4[b] | | | | 3420 |
| 2 | Mature grain[c] | HPLC | 23-27 | | 15-17 | | 3494 |
| 1 | –, endosperm[c] | HPLC | 391 | | | | 3379 |
| 1 | Leaf | IEC | 23.0 | | | | 2613 |
| 1 | Leaf[h] | Enzym. | 19.7 | 16.8 | 7.3 | 8.9 | 2574 |
| 1 | Mature leaf | Enzym. | 36.0 | 6.0 | 18.0 | 33.0 | 3495 |
| 1 | Leaf, midribs removed[a] | Enzym. | 7.5 | | 8.8 | | 3458 |
| 1 | Leaf, mesophyll chloroplast[g] | HPLC | | | 9.3 | 2.8 | 3496 |
| 1 | Sprout | IEC | + | | + | | 3497 |
| 1 | Sprout[a] | Enzym. | 74 | 0 | 38 | 1020 | 3408 |
| 1 | Sprout, embryo | HPLC | + | | | | 2760 |
| 1 | Seedling | Cyanide | 9.0 | | 5.5 | | 2656 |
| 1 | Seedling, endosperm[f] | Enzym. | 5.72 | 1.20 | 1.05 | 0.64 | 3411 |
| 1 | –, coleoptile[f] | Enzym. | 0.62 | 0.77 | 4.62 | 1.89 | 3411 |
| 1 | –, shoot[c] | Enzym. | 112 | 44.6 | 245 | 282 | 3422 |
| 1 | –, root | Enzym. | 129.5 | 38.4 | 6.1 | 150.0 | 3498 |
| 1 | Root tip | Enzym. | 123.5 | 12.9 | 7.6 | 10.7 | 3499 |
| 1 | Root tip[f] | HPLC | 0.63 | | | | 2759 |
| 1 | Root tip | $^{31}$P NMR | + | | | | 544 |
| 1 | Apical root[a] | Fluor. | 27 | | 30 | | 3500 |
| 1 | –, meristem[a] | Fluor. | 45 | | 20 | | 3500 |

*nmol/g fresh weight basis unless stated otherwise.
[a]µg/g.
[b]Incl. NADP and NMN.
[c]Dry weight basis.
[d]nmol/$10^7$ cells.
[e]Including NADH.
[f]nmol/plant part.
[g]nmol/mg chlorophyll.
[h]µmol/$m^2$.
[i]nmol/mg protein.
[j]Relative to brewer's yeast cozymase = 100.
[k]pmol/seedling.
[l]µmol/mg chlorophyll.
[m]Including NADPH.
[n]Based on its degradation product, ADPRib 2′ = phosphate.
[o]Cozymase units.
[p]nmol/−$10^9$ plastids.
[q]µmol/mmol chlorophyll.
[r]m*M*.
[s]µg/seedling.
[t]ng/g.

Gibbs energy of formation ($\Delta_f G$) −418.40 kJ/mol.[3538] *Trihydrate*: Needles or flat prisms (fig.), mp 140-142 °C dec.[3539] *Tetrahydrate*: Triclinic crystals, X-ray structure.[3540]
$LiC_{21}H_{26}N_7O_{14}P_2{\cdot}2H_2O$: Orthorhombic crystals (fig.), fp 203-204 °C, X-ray structure[3541]; $d_c$ 1.648.[3542]
$(C_{20}H_{24}N_2O_3)_3(C_{21}H_{27}N_7O_{14}P_2)_2$ (quinine salt): Needles (fig.), mp 162-170 °C dec.; UV (260 nm, ε 9.43), PE.[3543]

Nicotine adenine dinucleotide, reduced form (NADH), $C_{21}H_{29}N_7O_{14}P_2$, also called reduced Diphosphopyridine Nucleotide (DPNH). *Adenosine 5′-(Trihydrogen Diphosphate), P′→5′ Ester with 1,4-Dihydro-1-β-D-ribofuranosyl-3-pyridinecarboxamide*.

NADH [R.N. 58-68-4]: Colorless but turns yellow on exposure to moist air; solubility in 1,2-propanediol 15 mg/mL.[3544] Solutions in phosphate buffer at pH 7.4 are more stable at 4 °C than at 25 °C or frozen,[3545] but tris buffer is preferred to phosphate buffer.[3546] Fluorescence,[3547] phosphorescence (fig.),[2920] molecular self-association,[3508] molar absorptivity (ε) $6.18\times10^3$ L/mol/cm (334 nm, 25 °C),[3548] diamagnetic susceptibility ($\chi_M$) $-341\times10^{-6}$ cm$^3$/mol at 25 °C,[3510] ODMR.[2920] Ionization constant: p$K_a$ 3.88 (potentiometric, 25 °C).[3549] Spectra: UV (fig.),[3519] Raman (fig.),[3521] UV Raman (fig.),[3522] [$^1$H] NMR (fig.),[3523,3524] [$^{13}$C] NMR (fig.),[359] [$^{15}$N] NMR (fig.),[3525] [$^{31}$P] NMR (fig.),[3505] ORD (fig.),[2923] CD (fig.),[3550] LID-MS (fig.).[3529] Chromatography: PC,[3530] TLC,[3531] HPTLC,[2891] IEC,[3544] HPLC,[3544] DEAE cellulose column.[3533] Electrophoresis: PE,[9] CZE,[3534] capillary isotachophoresis.[3239] Theoretical calculations: LCAO-MO,[3536,3537] Gibbs energy of formation ($\Delta_f G$) −397.51 kJ/mol.[3538]
$Na_2C_{21}H_{27}N_7O_{14}P_2$: Fluorescence kinetics.[3551] Spectra: FAB-MS (fig.),[3528] FD-MS (fig.).[3528]
$BaC_{21}H_{27}N_7O_{14}P_2{\cdot}4H_2O$: Faintly yellow solid, $UV_{max}$ 340 nm.[3552]

Nicotine adenine dinucleotide phosphate (NADP), $C_{21}H_{28}N_7O_{17}P_3$, also called triphosphopyridine nucleotide (TPN). *Adenosine 5′-(Trihydrogen Diphosphate), 2′-(Dihydrogen Phosphate), P′→5′ Ester with 3-(Aminocarbonyl)-1-β-D-ribofuranosylpyridinium, Inner Salt*.

NADP [53-59-8]: Countercurrent distribution,[3511] diamagnetic susceptibility ($\chi_M$) $-370\times10^{-6}$ cm$^3$/mol at 25 °C,[3510] polarography,[3515] cyclic voltammetry (fig.).[3514] Ionization constants: p$K_a$ 3.874. 6.255 (potentiometric, 25 °C),[3553] 6.40 (2′-phosphate,[31]P NMR, 25 °C).[3554] Spectra: $^1$H NMR,[3523,3524] [$^{13}$C] NMR (fig.),[359] [$^{31}$P] NMR (fig.),[3505] CD (fig.),[3526] ESI-MS (fig.).[2887] Chromatography: PC,[3530] TLC,[3531] HPTLC,[2891] IEC,[2894] HPLC,[2440] DEAE cellulose column,[3533] GFC.[3555] Electrophoresis: PE,[9] CZE,[3534] capillary isotachophoresis,[3239] MECC.[3535] Theoretical calculations: Gibbs energy of formation ($\Delta_f G$) −418.40 kJ/mol.[3538]
$Na_2C_{21}H_{26}N_7O_{17}P_3$: FAB-MS (fig.).[3528]

Nicotine adenine dinucleotide phosphate, reduced form (NADPH), $C_{21}H_{30}N_7O_{17}P_3$. Also called reduced triphosphopyridine nucleotide (TPNH). *Adenosine 5′-(Trihydrogen Diphosphate), 2′-Dihydrogen Phosphate, P′→5′ Ester with 1,4-Dihydro-1-β-D-ribofuranosyl-3-pyridinecarboxamide*

NADPH [R.N. 53-57-6]: Somewhat stable in aqueous solution at pH 8 and above but sensitive to changes in temperature, ionic strength, and buffer salts. It has a shorter half-life than NADH under most conditions. Phosphorescence,[3556] molar absorptivity $\varepsilon = 6.18 \times 10^3$ L/mol/cm (334 nm, 25 °C);[3548] Gibbs energy of formation ($\Delta_f G$) −396.53 kJ/mol.[3538] Ionization constant: p$K_a$ 6.52 (2′-P, $^{31}$P NMR, 25 °C).[3554] Spectra: $^1$H NMR (fig.),[3523,3524] [$^{13}$C] NMR (fig.),[359] [$^{31}$P] NMR (fig.).[3505] Chromatography: PC,[3530] TLC,[3531] IEC,[2894] HPTLC,[2891] DEAE cellulose column.[3533] Electrophoresis: CZE,[3534] capillary isotachophoresis.[3239]

## Conformation

The conformation of NAD is folded in the free acid form, both in the crystalline state and in solution, but extended in its complexes with enzymes. In the free acid, each phosphate carries a negative charge, nicotinamide is positively charged at N-1, and adenine is protonated at N-1. The conformation of the free acid is similar to that of AMP with respect to its components—*anti* across the glycosidic bonds, *gg* across the $C_4'$—$C_5'$ bonds of the two bases, *endo* pucker at $C_2'$ in both riboses, and *trans* to $C_4'$ for both phosphates. The crystal structure exhibits a novel intermolecular stacking of adenine and water molecules on opposite sides of the nicotinamide resulting in a nicotinamide sandwich.[3540] In contrast, the lithium salt $Li^+NAD^+ \cdot 2H_2O$ has an extended conformation, similar to, but distinctly different from, that of NAD in its enzyme complexes. The lithium ion forces the molecule to adopt a conformation in which the NAD molecules are stacked head to tail.[3541,3542] These conformations are supported by detailed studies of the UV,[3557] [$^1$H] NMR,[3558] [$^{13}$C] NMR,[3559] [$^{31}$P] NMR,[3505] and CD[3526] spectra and by theoretical calculations using semiempirical[3560] and *ab initio* MO[3561] methods and by modular dynamics simulations.[3562] The existence of right- and left-handed conformers of the folded form has been discounted.[3558]

The conformation of NADH in aqueous solution has one folded structure similar to that of NAD in rapid equilibrium with an open (extended) form. The 1,4-dihydropyridine ring in the folded form is folded against the adenine in such a manner that the ring is puckered, $H_A$ is axial, and $H_B$ is equatorial. The bases move apart if the temperature is raised, the pH is lowered, or the polarity of the solvent is reduced.[3558] These results are supported by $^{31}$P NMR studies.[3505]

The conformations of NADP and NADPH in aqueous solution are primarily folded.[3523,3558] The ribose rings in NADP, according to $^1$H, $^{13}$C, and $^{31}$P NMR analysis, are almost equally distributed between 2′-*endo* and 3′-*endo* modes in the AMP component but are predominantly in the 2′-*endo* mode in the NMN component. The conformations about the bridging C(5′)—O(5′) and C(4′)—C(5′) bonds resemble those of the corresponding mononucleotides.[3563]

## Synthesis

NAD may be prepared (a) by condensation of NMN with AMP in the presence of dicyclohexylcarbodiimide,[3564] di-*p*-tolylcarbodiimide,[3565] or trifluoroacetic anhydride,[3566] (b) by reaction of NMN with an AMP morpholide[3567] or di-*n*-butylphosphinothioic

anhydride[2989] but not from $AMPNH_2$[3568] or (c) from NMN and ATP by the combined action of the enzymes NAD pyrophosphorylase and $PP_i$ pyrophosphatase.[3569]

NADH may be prepared from NAD (a) by chemical reduction with sodium hydrosulfite[3552] or sodium cyanoborohydride,[3570] (b) by electrolytic reduction with mercury,[3571] or (c) by enzymic reduction with yeast alcohol dehydrogenase and ethanol.

NADP may be prepared (a) by condensation of NMN with 2′,5′-ADP in the presence of dicyclohexylcarbodiimide[3564] or (b) by enzymic phosphorylation of NAD with ATP in the presence of NAD kinase.[3569]

NADPH may be prepared from NADP (a) by chemical reduction with sodium cyanoborohydride[3570] or (b) by electrolytic reduction with mercury.[3571] Sodium borohydride cannot be used for the preparation of NADH or NADPH because it produces a mixture of 1,2-, 1,4-, and 1,6- isomers.[3572]

## Hydrolysis

NAD is stable to acid but unstable to base. Dilute alkali (0.1-1.0*N* NaOH) splits the nicotinamide-ribose linkage, which is followed by splitting of the pyrophosphate group, releasing nicotinamide and adenylic acid, respectively.[3573] Stronger alkali (5*N* NaOH) results in the formation of a bluish fluorescent product, $\lambda$ 360 nm, subsequently identified as 2-hydroxynicotinaldehyde.[3574] The hydrolysis is second-order (pH-dependent) between pH 8.5 and 11 but becomes first-order (pH-independent) below pH 6.5 and above pH 12.5.[3518] The $pK_{eq}$ for the pH-dependent reaction is 11.7 at 37 °C, close to the $pK_a$ of the ribose diols (12.17 for C-2′, 12.13 for C-3′ at 20 °C), which suggests that cleavage of the nicotinamide-glycosyl bond is facilitated by the ionization of the adjacent ribose diol. A mechanism for the hydrolysis involving an oxocarbenium intermediate[3518] is supported by recent studies.[3575] For further details see Oppenheimer.[3576] Hydrolysis of NAD in the presence of $Zr^{4+}$ catalyst results in selective cleavage of the pyrophosphate bond giving NMN and AMP, a reaction previously possible only with the enzyme NAD pyrophosphorylase.[3577]

NADH, in contrast to NAD, is stable to base and unstable to acid. The degradation of NADH in unbuffered acid solution is initiated by a general acid-catalyzed hydration of the 1,4-dihydronicotinamide ring, followed by β to α anomerization of the nicotinamide-ribose bond and cyclization, forming a new oxazolidine ring.[3578] The hydrolysis is pH-dependent at moderately low pH but becomes pH-independent at very low pH and at high pH (9-12). The rate changes if a buffer is present owing to further interaction between the buffer and the 1,2-dihydronicotinamide ring. The reaction of NADH with potassium orthophosphate in aqueous solution, for example, results in a series of three consecutive second-order reactions, each of which gets completed before the next step begins.[3579] Prolonged hydrolysis of NADH with 6N HCl at reflux results in a 36.8% conversion to glycine owing to incomplete degradation of the adenosine ring.[3580]

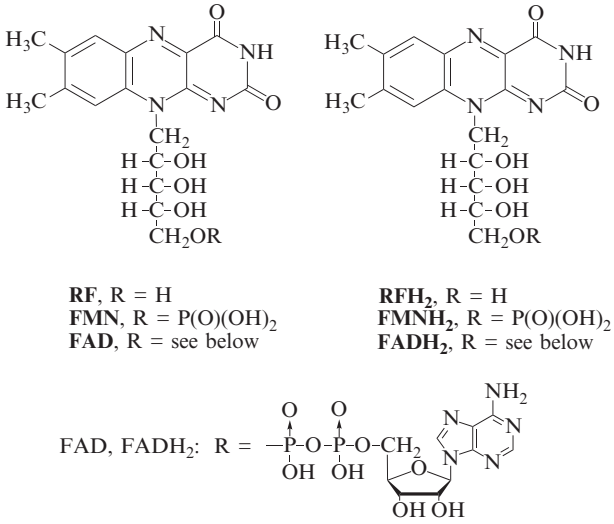
Hydrolysis of NADP under mild conditions (0.02*M* NaOH, 100 °C) splits the nicotinamide-ribose bond giving nicotinamide and ADPR 2′-phosphate,[3581] together with small amounts of ADP 2′-phosphate and AMP 2′-phosphate.[3582]

Like NADH, hydrolysis of NADPH in weakly acidic buffers follows first-order kinetics, but the rate is considerably greater at a given pH. The rate lines converge at very acidic pH.[3583]

For the effects of time, temperature, pH, and salts on the stability of NAD, NADH, NADP, and NADPH in aqueous solution, see Lowry *et al.*[3418]

# Riboflavin Nucleotides

This group comprises the riboflavin derivatives flavin mononucleotide (FMN), flavin adenine dinucleotide (FAD), and the corresponding dihydro derivatives.




## Occurrence

Since the late 1930s, it has been known that Riboflavin (vitamin $B_1$) is widespread in plants, especially in leafy vegetables, but its true nature was not revealed until the 1950s when Whatley[3406] isolated FAD from the leaves of clover, chickweed, potato, elder, and runner beans and Bevilacqua[3584] showed that the acid soluble "riboflavin" extracted from seeds or seedlings of wheat, oats, and other plants comprises FMN and FAD exclusively and contains no free riboflavin (RF) at all. During germination most of the FAD is found in the radicle and most of the FMN in the plumule.[3585] On the basis of this and other evidence, Appaji Rao and his group, who isolated and characterized all the enzymes listed in Fig. 6-2, concluded that the site of synthesis of the flavins was the radicle.[3585]

The metabolic pathways for the biosynthesis of the riboflavin nucleotides are outlined in Fig. 6-2. In step 1, riboflavin is phosphorylated by ATP giving FMN and ADP.[3586] In step 2, FMN reacts with ATP in the presence of FAD pyrophosphorylase giving FAD and $PP_i$.[3587] This pathway was confirmed by Koop and Barz,[3588] who found that [2-$^{14}$C]riboflavin is incorporated stepwise into FMN and FAD in mung bean, chickpea, and parsley cell

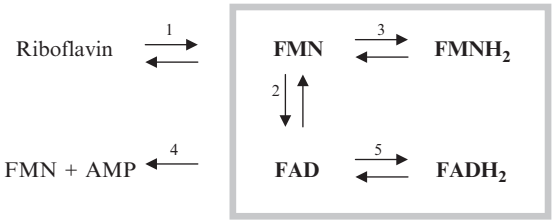



**FIGURE 6-2 Riboflavin Nucleotides**. (1) Riboflavin kinase [E.C. 2.7.1.26], ATP. (2) FAD pyrophosphorylase [E.C. 2.7.7.2], ATP. (3, 5) FMN reductase [E.C. 1.6.8.1], NAD(P)H. (4) FAD pyrophosphatase [E.C. 3.6.1.18], $H_2O$.

suspension cultures. In steps 3 and 5, FMN and FAD interact with NADH or NADPH giving $FMNH_2$ and $FADH_2$, respectively. In step 4, FAD is hydrolyzed by FAD pyrophosphatase giving FMN and AMP.[3589] There appears to be no enzymatic mechanism for salvage of the reduced nucleotides other than by way of returning to their oxidized forms.

The source of the riboflavin in plants is unknown. In bacteria, the building blocks for its biosynthesis are known to be guanosine 5′-triphosphate (GTP) and ribulose 5-phosphate (Ru5P), assembled through a series of seven enzyme-linked reactions.[3590]

## Extraction

Methods recommended by the AOAC, AACC, and other groups for the extraction of riboflavin from foodstuffs, clinical samples, and pharmaceuticals are too harsh for use in the determination of FMN and FAD.[3591] Extraction with ice-cold trichloroacetic acid under the conditions normally used for other nucleotides can be used for the simultaneous assay of RF, FMN, and FAD. An example of this procedure is described later in the fluorometric method. Several investigators have obtained good results with aqueous extraction using pH 7.4-7.7 phosphate buffer.[3452,3592,3593] Treadwell and Metzler[3594] used saturated ammonium sulfate as both extractant and protein precipitant.

## Separation

### *(a) From Acid Extracts*

Whatley[3406] used the procedure of Warburg and Christian[3595] in which ammonium sulfate is added to precipitate the protein and the FAD is separated from the other nucleotides by extraction of the supernatant with liquid phenol and precipitation with acetone. Sanwal and Waygood[3596] separated FMN and FAD from the other nucleotides by adsorption on Florisil and elution with aqueous pyridine.

### *(b) From Neutral Extracts*

Koziolowa[3597] and Koziol[3593] separated RF, FMN, and FAD in phosphate buffer extracts of whole wheat, flour, bran, and gluten by ion exchange chromatography on a sulfonic acid cation exchange resin (K-28, $H^+$ form). Van Gestelen *et al.* separated the flavins in phosphate buffer extracts of bean[3598] and corn[3599] plasma membranes by high-performance liquid chromatography using a reversed-phase column (Bio-Sil $C_{18}$ HL 90-5s).

## Analysis

### *(1) Enzymatic Method*

This method is based on reactivation of the enzyme D-amino acid oxidase [E.C. 1.4.3.3] when its prosthetic group (FAD) is restored after being removed by treatment with acid. The uptake of oxygen catalyzed by the reactivated oxidase upon the addition of the plant extract serves as a measure of its FAD content.[3406]

### *(2) Fluorometric Method*

Most of the analyses reported in Table 6-3 were carried out by the method developed by Bessey *et al.*[3612] for the determination of RF, FMN, and FAD in animal tissue. The following is a typical procedure applied to a plant tissue:

> *Tissue from tobacco plants was ground in an Omni mixer (Ivan Sorvall, Inc., Norwalk, Conn.) with 20 times its volume of ice water and mixed immediately with an equal volume of 20 per cent trichloroacetic acid. After centrifuging, an aliquot of the supernatant was neutralized with 4*M *$K_2HPO_4$. A second aliquot of the solution was stored in the dark at 38 °C. overnight to produce hydrolysis of FAD to FMN. After hydrolysis this sample was neutralized with $K_2HPO_4$. FAD was determined by differences in the fluorescence between the hydrolyzed and unhydrolyzed sample as outlined by Bessey* et al.[3612] *Free riboflavin was determine by shaking an aliquot of the unhydrolyzed sample with equal volumes of water-saturated benzyl alcohol. An aliquot of the benzyl alcohol layer was mixed with an equal volume of water, which was 0.05*M *with respect to sodium acetate and acetic acid, and 15 volumes of water-saturated toluene. An aliquot of the aqueous layer was then assayed fluorometrically for riboflavin.*[3612] *FMN was calculated by subtracting FAD and free riboflavin from total riboflavin.*
>
> Welkie, G. W.; Miller, G. W., "Iron Nutrition of *Nicotiana tabacum* L. in Relation to Riboflavin, Riboflavin-5-Phosphate and Flavin Adenine Dinucleotide Content", *Plant Physiol.* **1960**, *35*(4), 516–520,[3608] reprinted by permission of the American Society of Plant Biologists, © 1960.

Swaraj *et al.*[3592] used a modification of this method in which FMN and FAD are determined on the same sample at different pH values.[3613]

## Some Comments on the Reduced Flavins

The reader may have noticed the absence of data in Table 6-3 for $FMNH_2$ or $FADH_2$. The reasons for this are not hard to find. Both substances are extraordinarily air-sensitive, being readily reoxidized to FMN and FAD, respectively. All of the flavins are light-sensitive and need to be handled in subdued light, preferably in the dark. On the other hand, none of them exhibit the pH-sensitivity that is characteristic of the pyridine nucleotides discussed earlier in this chapter. The FMN/$FMNH_2$ couple is stable over the 0.85-12.95 pH range[3614,3615] and the FAD/$FADH_2$ couple over the 2.4-12.4 pH range.[3615] Decomposition products such as lumichrome and lumiflavin, which develop in acid and alkaline solutions, respectively, are the result of photodegradation and not of any inherent instability of the flavins.

**Table 6-3** Riboflavin (RF) Nucleotides in Plants*

| No. | Plant part | Method | Free RF | FMN | FAD | References |
|---|---|---|---|---|---|---|
| *Avena sativa* L. (Oats) | | | | | | |
| 2 | Seed[a] | Fluor. | | 0.48[b] | 0.41 | 3600 |
| 1 | –, endosperm[a] | Fluor. | 0 | 0 | 0.55 | 3600 |
| 1 | Seed[a] | Fluor. | | 0.41 | 0.09 | 3584 |
| 1 | Sprout[a] | Fluor. | | 1.56 | 0.56 | 3584 |
| 1 | Seedling, leaf[a] | Fluor. | 1.2 | 6.5 | 15.3 | 3601 |
| 1 | –, endosperm[a] | Fluor. | | 0.8[b] | 3.7 | 3600 |
| 1 | –, root[a] | Fluor. | | 6.6[b] | 5.0 | 3600 |
| 1 | , coleoptile | Fluor. | | 24.0[c] | | 3602 |
| | | and variation from tip to base | | | | |
| 1 | Shoot, etiolated | TLC | + | 0 | 0 | 3594 |
| *Beta vulgaris* L. (Beet) | | | | | | |
| 1 | Root | TLC | + | 0 | 0 | 3594 |
| *Brassica chinensis* L. (Chinese Colza) | | | | | | |
| 1 | Pollen, mature | | 0 | 10.98 | 3.92 | 3603 |
| 1 | –, immature | | 0 | 2.90 | 10.60 | 3603 |
| 1 | –, senescent | | 11.96 | 1.74 | 0 | 3603 |
| *Camellia japonica* L. (Camellia) | | | | | | |
| 1 | Pollen, mature | | + | 8.34 | 0.96 | 3603 |
| 1 | –, immature | | 0 | 3.26 | 4.94 | 3603 |
| 1 | –, senescent | | 5.92 | 3.08 | 0 | 3603 |
| *Camellia sinensis* L. (Tea) | | | | | | |
| 1 | Pollen, mature | | + | 11.34 | 1.36 | 3603 |
| 1 | –, immature | | 0 | 4.48 | 8.42 | 3603 |
| 1 | –, senescent | | 5.76 | 6.24 | + | 3603 |
| *Chaenomeles japonica* (Thunb.) [Lindl. ex] Spach (Japanese Quince) | | | | | | |
| 1 | Pollen, mature | | 0 | 6.07 | 2.53 | 3603 |
| 1 | –, immature | | 0 | 0.95 | 5.95 | 3603 |
| 1 | –, senescent | | 4.16 | 2.74 | 0 | 3603 |
| *Chlorophytum comosum* (Thunb.) Jacq. (Spider Plant) | | | | | | |
| 1 | Leaf[d] | Fluor. | | 50[b] | 94 | 3604 |
| *Cicer arietinum* L. (Bengal Gram) | | | | | | |
| 1 | Seed[a] | Fluor. | n.d.[e] | 0.41 | 0.57 | 3585 |
| *Coix lacryma-jobi* L. (Job's Tears) | | | | | | |
| 1 | Shoot, etiolated | TLC | + | 0 | 0 | 3594 |
| *Cosmos* spp. (Aster) | | | | | | |
| 1 | Pollen, mature | | 0 | 13.06 | 3.54 | 3603 |
| 1 | –, immature | | 0 | 3.68 | 8.72 | 3603 |
| 1 | –, senescent | | 8.92 | 5.08 | 0 | 3603 |
| *Daucus carota* L. (Carrot) | | | | | | |
| 1 | Root | TLC | + | 0 | 0 | 3594 |
| 1 | Root[f] | Enzym. | 0.10 | 0.04 | 0.42 | 3605 |
| *Glycine max* (L.) Merr. (Soybean) | | | | | | |
| 1 | Whole bean[f] | Enzym. | 0.15 | 0.90 | 1.62 | 3605 |
| 1 | Hypocotyl, tonoplast[g] | Fluor. | | | 2.0 | 3606 |

**Table 6-3** Riboflavin (RF) Nucleotides in Plants*—cont'd

| No. | Plant part | Method | Free RF | FMN | FAD | References |
|---|---|---|---|---|---|---|
| 1 | –, plasma membrane[g] | Fluor. | | | 0.5 | 3606 |
| 1 | Root nodule[g] | Fluor. | | 1.2 | 3.8 | 3592 |
| *Gossypium herbaceum* L. (Levant Cotton) | | | | | | |
| 1 | Seed | TLC | + | 0 | 0 | 3594 |
| *Helianthus annuus* L. (Sunflower) | | | | | | |
| 1 | Pollen, mature | | 0 | 14.31 | 4.49 | 3603 |
| 1 | –, immature | | 0 | 2.44 | 14.36 | 3603 |
| 1 | –, senescent | | 4.16 | 2.74 | 0 | 3603 |
| *Hizikia fusiformis* Harvey (Hijiki) | | | | | | |
| 1 | Air-dried plant | Fluor. | | | 6.0 | 3607 |
| *Hordeum vulgare* L. (Barley) | | | | | | |
| 1 | Seedling, leaf [a] | Fluor. | 7.3 | 7.7 | 7.5 | 3601 |
| 2 | Seedling, coleoptile (1) | Fluor. | | 10.6[c] | | 3602 |
| | Seedling, coleoptile (2) | Fluor. | | 30.0[c] | | 3602 |
| | | and variation from tip to base | | | | |
| *Ipomoea batatas* (L.) Lam. (Sweet Potato) | | | | | | |
| 1 | Tuber | TLC | + | 0 | 0 | 3594 |
| 1 | Tuber[f] | Enzym. | 0.90 | 0.03 | 0.87 | 3605 |
| *Lablab purpureus* (L.) Sweet (Hyacinth Bean) | | | | | | |
| 1 | Seed[a] | Fluor. | n.d.[e] | 0.58 | 1.43 | 3585 |
| *Laminaria japonica* Aresch. (Brown Seaweed) | | | | | | |
| 1 | Air-dried plant | Fluor. | | | 2.2 | 3607 |
| *Lilium longiflorum* Thunb. (Trumpet Lily) | | | | | | |
| 1 | Pollen, mature | | 0 | 9.80 | 4.50 | 3603 |
| 1 | –, immature | | 0 | 1.35 | 11.25 | 3603 |
| 1 | –, senescent | | 4.67 | 3.84 | 0.99 | 3603 |
| *Lycopersicon esculentum* Mill. (Tomato) | | | | | | |
| 1 | Stem | Fluor. | | | + | 3452 |
| 1 | Leaf | Fluor. | | | + | 3452 |
| 1 | Leaf | Fluor. | | 0.073[b] | 0.051 | 3596 |
| *Macrotyloma uniflorum* (Lam.) Verdc. (Horse Gram) | | | | | | |
| 1 | Seed[a] | Fluor. | n.d.[e] | 0.51 | 0.76 | 3585 |
| *Magnolia* × *soulangiana* Soul.-Bod. (Chinese Magnolia) | | | | | | |
| 1 | Leaf | TLC | + | 0 | 0 | 3594 |
| *Nicotiana tabacum* L. (Tobacco) | | | | | | |
| 1 | Leaf[a] | Fluor. | 1.4 | 0.1 | 0.2 | 3608 |
| *Oenothera biennis* ssp. *grandiflora* (Large-Flowered Evening Primrose) | | | | | | |
| 1 | Pollen, mature | | + | 13.13 | 2.37 | 3603 |
| 1 | –, immature | | 0 | 4.34 | 9.56 | 3603 |
| 1 | –, senescent | | 6.67 | 6.23 | 0 | 3603 |
| *Oryza sativa* L. (Rice) | | | | | | |
| 1 | Flour[f] | Enzym. | 0.32 | 0.08 | 0.12 | 3605 |
| 1 | Flour[f] | Enzym. | 0.37 | 0.69 | 0.93 | 3605 |

*μg/g fresh weight basis, unless stated otherwise; [a]Dry weight basis; [b]Including RF; [c]Including FAD; [d]μg/g protein nitrogen; [e]Not detected; [f]μg/g; [g]nmol/mg protein; [h]pmol/mg protein.

*Continued*

**Table 6-3** Riboflavin (RF) Nucleotides in Plants*—cont'd

| No. | Plant part | Method | Free RF | FMN | FAD | References |
|---|---|---|---|---|---|---|
| *Phaseolus coccineus* L. (Scarlet Runner Bean) | | | | | | |
| 1 | Leaf | Enzym. | | | 0.11 | 3406 |
| *Phaseolus vulgaris* L. (Common Bean) | | | | | | |
| 1 | Seed[a] | Fluor. | n.d.[e] | 1.11 | 2.01 | 3585 |
| 1 | Seed[a] | Fluor. | | 0.65 | 0.29 | 3584 |
| 1 | Apical hook plasma membrane[i] | HPLC | | 470 | n.d.[e] | 3598 |
| 1 | Sprout[a] | Fluor. | | 1.11 | 0.82 | 3584 |
| 1 | Seedling | Fluor. | | 9.7[b] | 9.7 | 3609 |
| *Pisum sativum* L. (Peas) | | | | | | |
| 1 | Seed[a] | Fluor. | n.d.[e] | 1.20 | 0.90 | 3585 |
| 1 | Seed[a] | Fluor. | | 0.40 | 0.28 | 3584 |
| 1 | Sprout[a] | Fluor. | | 1.25 | 1.35 | 3584 |
| *Porphyra tenera* Kjell. (Nori) | | | | | | |
| 1 | Air-dried plant | Fluor. | | | 17.8 | 3607 |
| *Portulaca grandiflora* Hook. (Rose Moss) | | | | | | |
| 1 | Pollen, mature | | + | 12.76 | 1.84 | 3603 |
| 1 | –, immature | | 0 | 4.83 | 6.67 | 3603 |
| 1 | –, senescent | | 5.61 | 3.19 | 0 | 3603 |
| *Raphanus sativus* L. (Radish) | | | | | | |
| 1 | Leaf[f] | Enzym. | 1.72 | 0.65 | 1.58 | 3352 |
| 1 | Tuber[f] | Enzym. | 0.06 | 0.02 | 0.24 | 3352 |
| *Robinia pseudoacacia* L. (Black Locust) | | | | | | |
| 1 | Pollen, mature | | 0 | 11.33 | 2.57 | 3603 |
| 1 | –, immature | | 0 | 4.08 | 9.12 | 3603 |
| 1 | , senescent | | 7.09 | 2.81 | 0 | 3603 |
| *Sambucus nigra* L. (European Elder) | | | | | | |
| 1 | Leaf | Enzym. | | | 0.28 | 3406 |
| *Secale cereale* L. (Rye) | | | | | | |
| 1 | Seed[a] | Fluor. | | 0.76[b] | 0.31 | 3600 |
| 1 | –, endosperm[a] | Fluor. | | 0.38[b] | 0.37 | 3600 |
| 1 | Seedling, leaf[a] | Fluor. | 1.2 | 6.1 | 9.1 | 3601 |
| 1 | –, endosperm[a] | Fluor. | | 2.6[b] | 1.8 | 3600 |
| 1 | –, root[a] | Fluor. | | 8.7[b] | 6.2 | 3600 |
| *Solanum tuberosum* L. (Potato) | | | | | | |
| 1 | Tuber | TLC | + | 0 | 0 | 3594 |
| 1 | Tuber[f] | Enzym. | 0.06 | 0.66 | 0.42 | 3605 |
| 1 | Leaf | Enzym. | | | 0.27 | 3406 |
| *Spinacia oleracea* L. (Spinach) | | | | | | |
| 1 | Leaf | PE | + | + | + | 3594 |
| 1 | Leaf[f] | Enzym. | 2.28 | 0.68 | 1.01 | 3605 |
| 1 | –, chloroplast and mitochondria[f] | Enzym. | 0.26 | 0.33 | 0.73 | 3605 |
| 1 | –, cytosol[f] | Enzym. | 1.39 | 0.39 | 0.17 | 3605 |
| *Stellaria media* (L.) Vill. (Chickweed) | | | | | | |
| 1 | Leaf | Enzym. | | | 0.20 | 3406 |

**Table 6-3** Riboflavin (RF) Nucleotides in Plants*—cont'd

| No. | Plant part | Method | Free RF | FMN | FAD | References |
|---|---|---|---|---|---|---|
| *Trifolium repens* L. (White Clover) | | | | | | |
| 1 | Leaf | Enzym. | | | 0.42 | 3406 |
| *Triticum aestivum* L. (Wheat) | | | | | | |
| 1 | Seed[a] | Fluor. | | 0.25 | 0.17 | 3584 |
| 1 | Grain | IEC | 1.2 | 0.7 | 0.5 | 3597 |
| 1 | Flour | IEC | 0.38 | 0.73[c] | | 3593 |
| 1 | Flour [f] | Enzym. | 0.64 | 0.16 | 0.32 | 3605 |
| 1 | Bran[f] | Enzym. | 0.28 | 0.51 | 0.64 | 3605 |
| 1 | Bran | IEC | 0.73 | 1.03[c] | | 3593 |
| 1 | Gluten | IEC | 0.32 | 0.28[c] | | 3593 |
| 1 | Seedling, leaf[a] | Fluor. | 1.0 | 5.8 | 9.2 | 3601 |
| 1 | Seedling, leaf[f] | Enzym. | 1.06 | 0.13 | 0.92 | 3605 |
| 1 | Leaf[a] | Fluor. | 2 | 93 | 46 | 3610 |
| 1 | –, etiolated[a] | Fluor. | 5 | 53 | 108 | 3610 |
| 1 | Sprout[a] | Fluor. | | 1.55 | 0.20 | 3584 |
| 1 | Shoot, etiolated | TLC | + | 0 | 0 | 3594 |
| *Undaria pinnatifida* (Harvey) Sur. (Wakame) | | | | | | |
| 1 | Air-dried plant | Fluor. | | | 6.8 | 3607 |
| *Vicia faba* L. (Horse Bean) | | | | | | |
| 1 | Leaf[f] | Enzym. | 2.14 | 0.61 | 2.01 | 3605 |
| *Vigna angularis* (Willd.) Ohwi and Ohashi (Adzuki Bean) | | | | | | |
| 1 | Whole bean[f] | Enzym. | 0.01 | 0.45 | 1.06 | 3605 |
| *Vigna mungo* (L.) Hepper (Black Gram) | | | | | | |
| 1 | Seed[a] | Fluor. | n.d.[e] | 0.12 | 1.90 | 3585 |
| *Vigna radiata* (L.) Wilcz. (Green Gram) | | | | | | |
| 1 | Seed[a] | Fluor. | n.d.[e] | 0.10 | 3.30 | 3585 |
| *Vigna unguiculata* (L.) Walp. (Cowpea) | | | | | | |
| 1 | Seed[a] | Fluor. | n.d.[c] | 0.20 | 2.40 | 3585 |
| *Vitis* spp. (Grape) | | | | | | |
| 4 | Vine | Fluor. | | 0.32-0.36 | 0-0.16 | 3611 |
| *Zea mays* L. (Corn) | | | | | | |
| 1 | Shoot or seedling | TLC | + | 0 | 0 | 3594 |
| 1 | Root plasma membrane [h] | HPLC | 52 | 121 | 89.6 | 3599 |

*µg/g fresh weight basis, unless stated otherwise.
[a]Dry weight basis.
[b]Including RF.
[c]Including FAD.
[d]µg/g protein nitrogen.
[e]Not detected.
[f]µg/g.
[g]nmol/mg protein.
[h]pmol/mg protein.

## Physical Properties

Flavin mononucleotide (FMN), $C_{17}H_{21}N_4O_9P$. *Riboflavin 5′-(Dihydrogen Phosphate).*

FMN [R.N. 146-17-8]: Slightly hygroscopic, greenish-yellow substance, soluble in water, glacial acetic acid, phenol and *p*-cresol, insoluble in acetone and ether,[3616] and slightly soluble in ethanol.[3617] Countercurrent distribution,[3618] phosphorescence,[3619] dipole moment (D) 150 esu cm,[2939] molecular weight (sedimentation, 25 °C),[3620] diamagnetic susceptibility ($\chi_m$) $-226\times10^{-6}$ cm$^3$/mol at 25 °C,[410] redox potential ($E_M$) −0.205 V at pH 7.0 and 20 °C,[3614] cyclic voltammetry (fig.),[3621] polarography.[3622] Ionization constants, potentiometric: p$K_a$ 6.60, 10.12 (18-20 °C)[3623] or 10.35 (20 °C).[3614] Spectra: UV (fig.),[3623] IR (fig.),[3623] Raman (fig.),[3624] ORD (fig.),[3625] CD (fig.),[3626] magnetic CD (fig.),[3627] $^1$H NMR (fig.),[3628] $^{13}$C NMR (fig.),[2926] $^{15}$N NMR (fig.),[3629] $^{31}$P NMR,[68] ESR (fig.),[3630] ENDOR (fig.),[3631] SERS (fig.),[3632] photoacoustic spectrum (fig.),[3633] thermospray MS,[3634] ES-MS,[3634] LC-MS.[3634] Chromatography: PC,[3635] circular PC,[3636] TLC,[3637] IEC,[3638] silica gel column,[3639] GFC,[3555] MECC.[3535] Electrophoresis: PE,[3640] CZE.[3641] Thermodynamics: $\Delta_fG^\circ$, E′°.[447]

$NaC_{17}H_{20}N_4O_9P{\cdot}2H_2O$: Yellow crystals. Solubility in water (mg/mL): 112 at pH 6.9, 68 at pH 5.6, and 43 at pH 3.8.[3642a]

$C_{13}H_9N{\cdot}C_{17}H_{21}N_4O_9P{\cdot}0.5H_2O$ (acridine salt): Brownish yellow needles (photo), mp 217 °C dec., soluble in hot water and insoluble in ethanol and ether.[3643]

Dihydroflavin mononucleotide ($FMNH_2$), $C_{17}H_{23}N_4O_9P$. *Riboflavin 5′-(Dihydrogen Phosphate), 1,5-Dihydro.*

$FMNH_2$ [R.N. 5666-16-0]: Molecular weight (sedimentation, 25 °C),[3620] polarography.[3622] Ionization constant: p$K_a$ 6.72 (potentiometric, 20 °C).[3614] Spectra: UV (fig.),[3644] $^{13}$C NMR,[3645] $^{14}$N NMR,[3645] $^{31}$P NMR,[3646] laser-excitation transient absorption (fig.).[3647] Thermodynamics: $\Delta_fG^\circ$.[447]

Flavin Adenine Dinucleotide (FAD), $C_{27}H_{33}N_9O_{15}P_2$. *Riboflavin 5′-(Trihydrogen Diphosphate), 5′→5′-Ester with Adenosine.*

FAD [R.N. 146-14-5]: Bright yellow hexagonal crystals (photo),[3648] soluble in water, pyridine, phenol, and *p*-cresol and insoluble in acetone, ether, ethanol, and chloroform.[3616] Phosphorescence,[3619] diamagnetic susceptibility ($\chi_m$) $-416\times10^{-6}$ cm$^3$/mol at 25 °C,[3510] countercurrent distribution,[3612] redox potential ($E_M$) −0.219 V at pH 7.0 and 30 °C,[3615] INDO charge density calc.,[3649] polarography,[3622] CCSA polarography (fig.),[3650] cyclic voltammetry (fig.).[3651] Spectra: UV-Vis. (fig.),[3649] Raman (fig.),[3624] FTIR (fig.),[3651] ORD (fig.),[3625] CD (fig.),[3626] magnetic CD (fig.),[3652] $^1$H NMR (fig.),[3653] 2d-$^1$H NMR (fig.),[3654] $^{13}$C NMR (fig.),[2926] $^{15}$N NMR (fig.),[3629] $^{31}$P NMR,[68] ESR,[3630] ENDOR (fig.),[3631] SERS (fig.),[3632] CIDNP (fig.),[3655] thermospray MS,[3634] ES-MS.[3634] Chromatography: PC,[3635] circular PC,[3636] IEC,[3638] HPLC,[3656] GFC,[3157] LC-MS,[3634] column (active carbon).[3657] Electrophoresis: PE,[3640] cellulose column,[3648] isotachophoresis.[3239] Thermodynamics: $\Delta_fG^\circ$, E′°.[447] Theoretical calculations: LCAO-MO,[3536] SCF-MO.[3658]

Ba $C_{27}H_{31}N_9O_{15}P_2$: Small yellow spheres in grapelike clusters, $UV_{max}$ 366, 445 nm.[3642b] Solubility in water, 2.5 g/L at 25 °C.[3595]

Dihydroflavin adenine nucleotide ($FADH_2$), $C_{27}H_{35}N_9O_{15}P_2$. *Riboflavin 5′-(Trihydrogen Diphosphate), 1,5-Dihydro, 5′→5′-Ester with Adenosine.*

$FADH_2$ [R.N. 1910-41-4]: Polarography,[3622] PSA polarography (fig.).[3650] Spectra: FTIR (fig.),[3651] laser-excitation transient absorption.[3647] Thermodynamics: $\Delta_f G^\circ$.[447] Theoretical calculations: MO (INDO method).[3659]

## Conformation

That strong interaction exists between the adenine and isoalloxazine rings of FAD is evident from the self-quenching of fluorescence compared to that of riboflavin or FMN.[3612] Proton NMR data indicate that the rings are hydrogen bonded to each other. A similar association occurs in aqueous solution between FMN and AMP (the components of FAD) but not between FMN and GMP or CMP.[3660]

In aqueous solution, FAD exists as an equilibrium mixture of open and folded conformers. This conclusion was reached by NMR analysis and confirmed by ORD measurements[3626] and MO calculations.[3658] In the folded conformation the two rings are vertically stacked, but the precise nature of the stacking is unclear; for a discussion of several proposed models see Kainosho and Kyogoku.[3628] The closed conformer also fluoresces but its lifetime (0.3 ns at room temperature) is very short.[3661]

Recent studies based on $^{13}C$ and $^{15}N$ NMR shift data suggest that the conformation of $FMNH_2$ is slightly bent about the $N_5$-$N_{10}$ axis in nonpolar solvents but almost planar in aqueous solution.[3645]

## Synthesis

FMN may be prepared (a) by phosphorylation of 2′,3′,4′-triacetylriboflavin with $POCl_3$ in pyridine,[3662] (b) by phosphorylation of unprotected riboflavin with metaphosphoric acid,[3663] monochlorophosphoric acid,[3664] *N*-morpholinophosphorodichloridate,[3665] or an alkyl phosphorodichloridate,[3666] (c) by oxidation of riboflavin 5′-phosphite with bromine or *N*-bromosuccinimide,[3667] or (d) by acid hydrolysis of riboflavin 4′,5′-phosphate.[3668]

$FMNH_2$ may be prepared (a) by catalytic hydrogenation of FMN in the presence of platinized asbestos,[3669] (b) by the reaction of FMN with dithionite,[3615] or (c) by phosphorylation of dihydroriboflavin with partially hydrolyzed $POCl_3$.[3670]

FAD may be prepared (a) by condensation of FMN with AMP in the presence of di-*p*-tolylcarbodiimide [3671] or trifluoroacetic anhydride,[3672] (b) by reaction of FMN with an AMP ester,[3123] amide,[3673] morpholide,[3674] imidazolide,[2993] or anhydride,[2989,3010] or (c) by reaction of FMN with an AMP derivative that contains 2′,3′-protecting substituents.[3399,3675]

$FADH_2$ may be prepared (a) by catalytic hydrogenation of FAD in the presence of platinized asbestos,[3622] or (b) by the reaction of FAD with dithionite.[3615]

## Hydrolysis

Hydrolysis of FMN to riboflavin and $P_i$ is the predominant reaction in the 2-7 pH range, reaching a maximum at pH 4 in common with other phosphate esters. At pH 4 and 80 °C, the rate constant is $6.48 \times 10^{-7}$ $s^{-1}$. Below pH 2, the predominant reaction is acid-catalyzed rearrangement; at pH 1 and 50 °C, the reaction mixture at thermodynamic equilibrium contains riboflavin and 5′-, 4′-, 3′-, and 2′-phosphates in the ratio 66:11:8:15. The rearrangement is pH-dependent, increasing linearly with the acid concentration.[3676] Prolonged hydrolysis of FMN in 1*N* HCl at 100 °C results in the formation of 2′,5′-anhydroriboflavin.[3677] Under much milder conditions (pH 8.6, 37 °C), the hydrolysis is catalyzed by Ce(III) and other heavy metal ions.[3678] Heating FMN in NaOH solution ruptures the isoalloxazine ring giving a keto acid.[3679]

## Phosphorylation

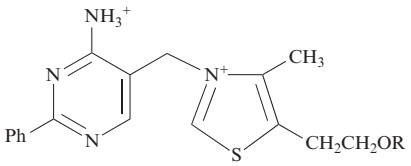
Condensation of FMN with phosphoric acid in the presence of *p*-tolylcarbodiimide results in a 17% conversion to riboflavin 5′-diphosphate. Use of the more reactive DCC produces only cyclic FMN.[3680]

# 7 Vitamins

This chapter is concerned with the vitamins thiamine ($B_1$) and pyridoxine ($B_6$) and their phosphates. For the vitamin riboflavin ($B_7$) and its phosphates, see Chapter 6. The Vitamin $B_1$ complex is considered first.

## Vitamin $B_1$

The Vitamin $B_1$ complex comprises thiamine and its monophosphate (TMP), thiamine di- or pyrophosphate (TDP, also known as cocarboxylase), and thiamine triphosphate (TDP).




**TMP**, R = $P(O)(O^-)_2$
**TDP**, R = $P(O)(O^-)OP(O)(OH)O^-$
**TTP**, R = $P(O)(O^-)OP((O)(OH)OP(O)(OH)O^-$

Thiamine Monophosphate (TMP), $C_{12}H_{17}N_4O_4PS$ [R.N. 495-23-8]; Beilstein **27** E IV 1776. *3-[(4-Amino-2-methyl-5-pyrimidinyl)methyl]-4-methyl-5-[(2-phosphonooxy)ethyl]thiazolium Betaine.*

Thiamine Di- or Pyrophosphate (TDP, Cocarboxylase), $C_{12}H_{18}N_4O_7P_2S$ [R.N. 136-09-4]; Beilstein **27** E IV 1777. *3-[(4-Amino-2-methyl-5-pyrimidinyl)-methyl]-4-methyl-5-(4,6,6-trihydroxy-3,5-dioxa-4,6-diphosphahex-1-yl)thiazolium Betaine P,P′-Dioxide.*

Thiamine Triphosphate (TTP), $C_{12}H_{19}N_4O_{10}P_3S$ [R.N. 15666-52-1]; Beilstein **27** E IV 1778. *3-[(4-Amino-2-methyl-5-pyrimidinyl)methyl]-4-methyl-5-(4,6,8,8-tetrahydroxy-3,5,7-trioxa-4,6,8-triphosphaoct-1-yl)thiazolium Betaine P,P′,P″-Trioxide.*

### Occurrence

Thiamine (vitamin $B_1$) is widely distributed in the higher plants as in other forms of life.[3681] The most abundant form in plant tissue is free thiamine, but it also occurs in varying degrees in the form of mono-, di-, and triphosphate esters. The diphosphate ester TDP, cocarboxylase, is an important coenzyme for pyruvate decarboxylase and pyruvate dehydrogenase in the Krebs cycle and for transketolase in the pentose shunt pathway, but TMP and TTP (like thiamine itself) exhibit no cocarboxylase activity.[3682] For a review of the catalytic functions of the thiamine phosphates, see Krampitz.[3683]

The discovery of cocarboxylase in plants dates to 1937, when Tauber[3684] found it to be present in a variety of vegetables, fruits, and nuts in amounts ranging from 0.4% to 30% of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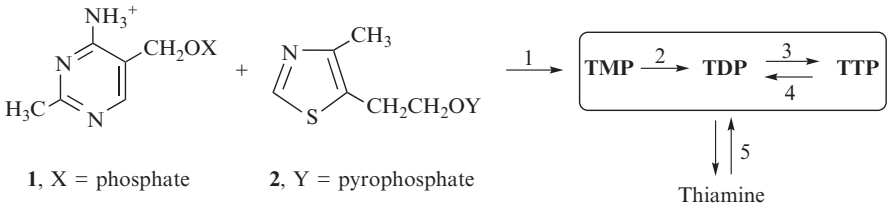



**FIGURE 7-1** Thiamine Phosphates. (1) TMP pyrophosphorylase [E.C. 2.5.1.3]. (2) TMP kinase [E.C. 2.7.4.16], ATP. (3) TDP kinase [E.C. 2.7.4.15], ATP. (4) Thiamine triphosphatase [E.C. 3.6.1.28]. (5) Thiamine pyrophosphokinase [E.C. 2.7.6.2], ATP.

the total thiamine content (Table 7-1). The presence of the other phosphorylated thiamine esters in plants was not established until 1961.[3685]

The metabolic pathways for the biosynthesis of the thiamine phosphates are outlined in Fig. 7-1. In step 1, TMP is formed by the coupling of (4-amino-2-methyl-5-pyrimidinyl) methyl pyrophosphate (**1**) and (4-methyl-5-thiazolyl)ethyl phosphate (**2**). In steps 2 and 3, TMP is phosphorylated to TDP and thence to TTP. Cell-free biosynthesis of **1** and **2** has not been established, but mechanistic sequences have been proposed for the biosynthesis of **1** from 5-aminoimidazole riboside, an intermediate on the purine biosynthetic pathway, and of **2** from 1-deoxyxylulose 5-phosphate (dXu5P), cysteine, and tyrosine.[3590]

## Physical Properties

Each of the phosphorylated thiamine derivatives can exist either as a betaine in which the two positive charges are balanced by negative charges on the phosphate residue or as a salt in which one or both positive charges are balanced by a stronger acid, usually HCl.

### Thiamine Monophosphate

TMP [R.N. 495-23-8]: Colorless rods, mp 228-230 °C dec., soluble in water (pH 5.5 for a 5% solution at 20 °C), insoluble in lower alcohols or acetone.[3686]
TMP·HCl: mp 193 °C dec., PE.[3687]
TMP·HCl·2$H_2O$ [R.N. 16028-14-1]: Large white plates, mp 200 °C, soluble in water, insoluble in ethanol[3688]; isoelectric pH 8.3[3689]; p$K_a$.[3690,3691] Spectra: UV,[3688] IR (fig.),[3692] fluorescence,[3693,3694] phosphorescence,[3693] $^1$H NMR,[3695] $^{13}$C NMR,[3696] $^{31}$P NMR (fig.).[3695] Chromatography: PC,[3697,3698] TLC,[3699,3700] IEC (Sephadex C-25,[3701] cellulose,[3697] starch[3697]), HPLC,[3702] Sephadex gel.[3703] Electrophoresis: Paper,[3697,3704] starch column,[3697] high-voltage zonal.[3705] Polarographic reduction: AC,[3691] DC.[3690,3706]
TMP·2HCl·2$H_2O$: mp 215-217 °C dec.,[3688] p$K_a$,[3707] TLC.[3700]

### Thiamine Diphosphate

TDP·4$H_2O$ [R.N. 136-09-4]: Triclinic prisms, mp 207 °C,[3708] d 1.542,[3708] 1.56,[3709] stable on storage.[3710,3711] Spectra: IR,[3712] $^1$H and $^{31}$P NMR.[3695] PC,[3710] IEC,[3710] X-ray structure,[3708,3709] high-voltage zonal electrophoresis.[3705]

TDP·4.5$H_2O$ [R.N. 71222-11-2]: Triclinic colorless tabular crystals, mp 232 °C, d 1.567, X-ray structure.[3713]
TDP·HCl: Rods, mp 239-240 °C dec.[3686]; monoclinic plates, d 1.656, X-ray structure.[3714] The cell dimensions do not allow for the 1/2 mol water of crystallization usually reported for this salt (see next entry).
TDP·HCl·1.5$H_2O$ [R.N. 154-87-0]: Nonhygroscopic white needles (photo[3692]), mp 242-244 °C,[3688] readily soluble in cold water, insoluble in alcohols and acetone, colorless in acid or neutral solution, yellow in alkaline solution,[3688] isoelectric pH 3.6,[3689] p$K_a$ (potentiometric),[3690,3715,3716] phase diagrams for $H_2O$ solutions exhibit eutectics for stable and metastable modifications at −0.8 and −2.3 °C, respectively.[3717] Spectra: UV,[3690,3718] IR (fig.),[3692,3719] fluorescence,[3693,3694] phosphorescence,[3693] $^1$H NMR,[3720] $^{13}$C NMR,[3696] $^{31}$P NMR,[3721,3722] DTA.[3723] Electronic structure calculations: MO,[3724] point charge.[3725] Chromatography: PC,[3697,3726] TLC,[3699] IEC (resin,[3697] Sephadex C-25[3701]), column (starch,[3697] cellulose,[3697] Norite[3727]), HPLC,[3702,3728] Sephadex gel,[3703,3729] GC.[3730] Electrophoresis: PE,[32,3697,3704] starch column.[3697] Polarography,[3690,3731,3732] oscillopolarography,[3733] fast cyclic voltammetry.[3734] Electron microscopy (photo).[3735]

### Thiamine Triphosphate

TTP·0.5$H_2O$ [R.N. 3475-65-8]: Crystals, mp 194 °C dec.,[3736] water soluble. Spectra: $^1$H NMR,[3737] luminescence.[3694] Chromatography: PC,[3697,3738] TLC,[3699] IEC (cellulose, starch),[3697] HPLC.[3702,3728] Electrophoresis: PE,[3697,3704] starch.[3697] Polarography.[3739]
TTP·2$H_2O$: Crystals, mp 194-197 °C dec.[3740]
TTP·HCl·$H_2O$ [R.N. 15666-52-1]: Short hygroscopic rods, mp 237-239 °C (photo), UV (fig.); PC,[3741] TLC,[3700] PE, cellulose column electrophoresis.[3741]

## Synthesis

TMP may be prepared (a) by phosphorylation of thiamine with pyrophosphoric acid,[3742] metaphosphoric acid,[3711] or polyphosphoric acid[3743]; (b) by hydrolysis of TDP with dilute HCl or $H_2SO_4$ at 100 °C[3688,3744,3745]; (c) by hydrolysis of TTP with dilute $Ba(OH)_2$ or piperazine at 0 °C[3746,3747]; or (d) by the reaction of 4-methyl-5-thiazoleethyl phosphate with 4-amino-5-bromomethyl-2-methylpyrimidine.[3687]

TDP may be prepared (a) by phosphorylation of thiamine with metaphosphoric acid,[3742,3748] polyphosphoric acid,[3743] or (in lower yield) pyrophosphoric acid[3749,3750]; (b) by the reaction of 4-methyl-5-thiazoleethyl diphosphate with 4-amino-5-bromomethyl-2-methylpyrimidine[3687,3742] or 4-amino-5-chloromethyl-2-methylpyrimidine[3751]; or (c) by metathesis between 5-bromothiamine and silver pyrophosphate.[3752]

TTP may be prepared by phosphorylation of thiamine with metaphosphoric acid[3748,3753] or phosphoric acid-phosphorus pentoxide.[3736]

The phosphorylation of thiamine invariably produces mixtures of mono-, di-, tri-, and polyphosphates in proportions that vary with the phosphorus content of the reagent.[3743]

The solubility of the products in ethanol decreases in the order thiamine > TMP > TDP > TTP.[3738] Separation of the mixture into its components is usually accomplished by ion exchange chromatography.[3697,3743]

## Conformation

The structures of TMP·$H_3PO_4$·$3H_2O$,[3754] TMP·$HPF_6$·$2H_2O$,[3755] and TDP·HCl[3714] have been determined by single crystal X-ray analysis. The geometry is similar to that of thiamine, with the thiazole and pyrimidine rings (both positively charged) almost at right angles to each other. The side chain is folded back over the thiazole ring in such a manner that the O(5γ) lone pair is directed toward the positively charged S(1). The inner phosphate group in TDP·HCl carries a negative charge. TDP itself crystallizes in two polymorphic forms: prismatic TDP·$4H_2O$ and tabular TDP·$4.5H_2O$.[3708,3713] Both show the same geometry as thiamine, but the pyrophosphate moiety extends away from the thiazole ring and each phosphate group in each polymorph carries a negative charge.

NMR studies on TDP in solution provide further evidence that the molecule can exist in both folded and extended conformations, depending on the metal ion used as the probe. Molecular orbital calculations on TDP in various states of ionization have been used to define the regions of preferred conformation.[3724] Quantum chemical point charge calculations have also been performed on TDP, its ylide, and some of its metal complexes.[3712]

## Hydrolysis

Aqueous solutions of the phosphorylated thiamines undergo the opening of the thiazole ring above pH 7 that is a characteristic of thiamine. The reaction is reversible but if the solution is allowed to stand in contact with air, the thiol may be oxidized irreversibly to the disulfide.[3690] In aqueous solution, the phosphorylated thiamines, like thiamine itself, are sensitive to irradiation by UV[3756] or X-rays.[3757,3758]

TMP is resistant to acid hydrolysis even at 100 °C, but becomes progressively less stable as the pH increases. Hydrolysis at pH > 5 is complicated by breakdown of the thiamine to degradation products that give a negative thiochrome reaction.[3690,3759] Under mildly alkaline conditions, the hydrolysis is catalyzed by La(III) and Ce(III).[3760]

Hydrolysis of TDP yields thiamine, TMP, or both, depending on the reaction conditions. Hydrolysis with dilute HCl or $H_2SO_4$ at 100 °C is a useful method for the preparation of TMP (p 443). Under alkaline conditions, the products are thiamine and pyrophosphoric acid.[3745] The hydrolysis is catalyzed by La(III) and Ce(III)[3760]; by Th(III), Zr(IV), Hf(IV), and Ti(IV)[3015]; and by Cu(II).[3761] For measurements of the kinetics under a variety of conditions, see refs. 3690,3762–3764. At all temperatures, TDP is most stable to hydrolysis at pH 6.0.[3763]

Hydrolysis of TTP at 100 °C gives mixtures of thiamine, TMP, and TDP, the ratio of pyrophosphate to phosphate increasing with pH.[3745] Pure TTP is most shelf-stable as the dilithium salt.[3765]

The first-order rate constants $k$ for the hydrolysis of TMP, TDP, and TTP at 100 °C are given in Table 7-1.[3745]

**Table 7-1** First-Order Rate Constants $k$ ($min^{-1}$)

| Compound | pH 1.0 | pH 7.2 | pH 8.7 |
|---|---|---|---|
| TMP | 0.002 | 0.009 | 0.081 |
| TDP | 0.033 | 0.014 | 0.025 |
| TTP | 0.130 | 0.012 | 0.008 |

## Phosphorylation

Phosphorylation of TMP or TDP with phosphoric acid in the presence of acetic anhydride or DCC invariably gave mixtures of TMP, TDP, and TTP and in some cases, thiamine polyphosphate.[3710,3766] With acetic anhydride alone at 0 °C, the product (not characterized) was the mixed acetic-phosphoric or acetic-pyrophosphoric anhydride.[3767] The reaction of TMP with adenosine (or inosine)-5′-phosphate and DCC in pyridine/DMF gave the mixed thiamine-adenosine (or inosine) diphosphate.[3768] For the reactions of thiamine, TMP, and TDP with other phosphorylating agents, see ref. 3766.

## Complex Formation

Divalent metal ions such as Mg(II) or Ni(II) react with TMP and TDP to form 1:1 complexes. The structures of these complexes are important in relation to the mechanisms of the interaction of cocarboxylase with enzymes, several of which require Mg(II) as a cofactor. $^1$H NMR data suggest that the metal ions in the TMP complexes are coordinated solely to the phosphate group,[3769,3770] but a single crystal X-ray analysis of the Rh(II) complex TMP·$Rh(OAc)_2$·$3/4H_2O$ showed that the TMP ligand is coordinated to the two axial positions of the $[Rh(OAc)_2]_2$ cage through the pyrimidine nitrogen N(1′).[3771] The conformation of the TMP ligand in the Rh(II) complex is folded like that of TMP·$H_3PO_4$ (p 444).

In most of the complexes with TDP, the metal is bonded exclusively to the pyrophosphate group. The conformation may be folded or unfolded, depending apparently on the extent of further interaction between the metal ion and the pyrimidine nitrogen N(1′). Thus, in the series $Ni(II) \gg Mn(II) > Mg(II)$, NMR studies indicate that in solution, the TDP is folded, partly folded, and unfolded, respectively.[3737,3769,3772,3773, but see ref. 3725] A single crystal X-ray analysis on the ternary complex TDP·phen·$Cu(NO_3)_2$·$2H_2O$ revealed a partly folded but on the whole rather extended conformation more akin to that of neutral TDP than to that of TDP·HCl.[3774]

The thiamine-binding proteins in seeds increase in amount during seed maturation and decrease during germination. For this form of complexing, which is beyond the scope of this book, see Kozik and Rapala-Kozik.[3775]

## Extraction, Separation, and Analysis

The vitamin $B_1$ content of plant tissues is usually measured by methods developed for animal tissues, for which a preliminary hydrolysis is necessary to liberate the thiamine from its protein- or phosphate-bound forms. Several methods have been developed in recent years for the separation and quantitative analysis of mixtures of thiamine and its mono-, di-, tri-, and polyphosphate esters. The best of these are paper chromatography (PC), ion exchange chromatography (IEC), and high-performance liquid chromatography (HPLC). The other methods described later are suitable if only TDP and total thiamine are required. For periodic reviews of these methods and their applications, see the sections on thiamine in *Methods in Enzymology*.[3776–3778]

In most cases, the final analysis is carried out by the thiochrome method after enzymatic hydrolysis to convert the thiamine phosphates in each fraction to free thiamine. The thiamine is then oxidized with potassium ferricyanide in NaOH solution and the fluorescence of the resulting thiochrome is measured in a fluorimeter set for excitation at 339 nm and emission at 432 nm. Two other rarely used methods are the Roussin salt fluorometric method described by Teysseire in method 2[3779] and the azo colorimetric method employed by Yusa in method 3b.[3780]

### *(1) Chromatographic Methods*

**(A) ION EXCHANGE CHROMATOGRAPHY (IEC)**

This was the first method that enabled all four compounds—thiamine, TMP, TDP, and TTP—to be determined simultaneously on a single plant sample.

> *A weighed sample containing about 15-30 μg of total T [thiamine] was extracted with cold 5% trichloroacetic acid solution, by homogenization, the extraction being twice repeated and the extracts centrifuged. The combined extracts, adjusted to pH 6.7-6.9, were passed through a column made up of a mixture of cholesteryl stearate-treated charcoal and cellulose powder, which retained T and its esters. After a washing with $H_2O$, T compounds were quantitatively eluted with aqueous propanol (9:1). After concentration to a small volume in a rotating evaporator at 37°C, the eluate, acidified to pH 4-4.5, was passed through a column of Dowex 1 resin, X8, 200-400 mesh (acetate form), which retained TDP and TTP and allowed T and TMP to pass through. T and TMP were then determined fluorometrically (thiochrome method) in the solution before and after incubation with acid phosphatase. TDP and TTP were subsequently eluted from the resin column with 0.02*M *and 1.0*M *acetate buffer solution, respectively, and determined in the same manner after incubation with acid phosphatase.*
>
> Rindi, G.; de Giuseppe, L., "Content of Thiamine and its Mono-, Di-, and Triphosphoric Esters in Different Biological Materials", *Int. Z. Vitaminforsch.* **1961**, *31*, 321–326,[3685] reprinted by permission of Verlag Hans Huber, © 1961.

**(B) PAPER CHROMATOGRAPHY (PC)**

The thiamine compounds were extracted with trichloroacetic acid and adsorbed on charcoal as described by Rindi and de Giuseppe.[3685] The eluate from the charcoal was treated

with 1 mL of 1*M* acetate buffer (pH 5.0), concentrated *in vacuo* to about 1 mL, separated by ascending paper chromatography using *n*-propanol/water/0.5*M* acetate buffer (pH 5.0) (7:2:1), and detected by the thiochrome method.[3780]

**(C) HIGH-PERFORMANCE LIQUID CHROMATOGRAPHY (HPLC)**

The thiamine compounds were extracted with 5% sulfosalicylic acid in the presence of amprolium as an internal standard. The eluate was passed through a column packed with Bio-Rad AG2-X8 anion-exchange resin to remove the sulfosalicylic acid, which fluoresces strongly and would interfere with the thiochrome detection. The solution was then injected into a Perkin-Elmer $C_{18}$ reversed-phase column and separated into its components by isocratic elution with 0.1*M* sodium phosphate buffer, using postcolumn conversion of the thiamines to their thiochrome derivatives. The thiamines eluted in the order TDP > TMP > thiamine. TTP was not found in any of the samples that were analyzed.[3781] The HPLC method was also employed in a study of TDP binding by seed proteins.[3775]

**(D) GEL FILTRATION CHROMATOGRAPHY (GFC)**

A 0.2-mL aliquot of the sample (wheat flour extract or orange juice) was transferred to a $10 \times 600$-mm Sephadex G-25 column and eluted with 0.1% $NaHSO_4$. The fraction (12 mL) containing the thiamines was analyzed for thiamine and TDP by the thiochrome method before and after extraction with amyl alcohol.[3729] This method does not distinguish between TDP and other amyl alcohol-insoluble thiamine phosphates.

### *(2) Teysseire Method*

The tissue, softened if necessary by soaking with three times its weight of water, was ground in a mortar with 40-50 g of anhydrous sodium sulfate, filtered, and rinsed three times with saturated ammonium sulfate. The filtrate was treated with 120-150 mg of $Na[Fe_4(NO)_7S_3]$ (Roussin's salt) and a few milliliters of 20% sodium benzoate solution and allowed to stand until the precipitation of salts was complete (15 h). The precipitate was collected on a filter, washed with water, and dried at 50 °C. The Roussin salt of thiamine was extracted from the precipitate with methylal and the Roussin salt of TDP with 95% ethanol. The salts were then analyzed separately for thiamine and TDP by a method developed by the authors[3782] based on the salts' absorption at 340 nm in the presence of strong alkali.[3779]

### *(3) Enzymatic Methods*

These methods make use of the enzymatic reactions shown in Table 7-2.

**Table 7-2** Enzymatic Reactions

| Method | Reaction | Enzyme |
|---|---|---|
| 3a | Pyruvate $\rightarrow$ acetaldehyde $+ CO_2$ | Pyruvate decarboxylase [E.C. 4.1.1.1] |
| 3b | TDP $+ 2H_2O \rightarrow$ thiamine $+ 2\ H_3PO_4$ | Acid phosphatase [E.C. 3.1.3.2] |

### (A) MANOMETRIC METHOD (MANOM.)

This method is based on the restoration of the activity of pyruvate decarboxylase (Table 7-2, reaction 3a) when TDP is reunited with the enzyme in acid-washed Baker's yeast. Thiamine itself has a stimulating effect on this reaction and can also be measured by this method, but this was not done for any of the studies cited in Table 7-3. The following procedure is typical:

> *The well ground plant tissue was extracted by boiling for 5 minutes with 3 to 5 times their weight of pH 6.239 Sörensen buffer. A 2 mL aliquot of the clear filtrate was treated with 1 mL of dry yeast that had been washed practically free of cocarboxylase, and incubated at 35° C in a Warburg apparatus with 0.5 mL of pyruvate/$MgCl_2$ solution as the substrate. The amount of $CO_2$ evolved in 60 min. was measured. Under these conditions, synthetic cocarboxylase liberated 56 $mm^3$ $CO_2$, equivalent to 5 μg vitamin $B_1$.*
>
> Tauber, H., "Co-Carboxylase (Vitamin $B_1$ Pyrophosphate) Content of Plants", *Proc. Soc. Exp. Biol. Med.* **1937**, *37*(3), 541–543,[3684] reprinted by permission of the Royal Society of Medicine Press, UK, © 1937.

### (B) PHOSPHATASE METHOD

Incubation of a plant extract with an acid phosphatase results in the quantitative conversion of all the thiamine present to the free form (Table 7-2, reaction 3b). Some phosphatases that have been employed for this purpose are Clarase,[3801] takadiastase,[3780,3796] and extracts of beef kidney,[3797] yeast,[3792] or wheat.[3790,3801] The concentration of phosphorylated thiamine is estimated by the difference between thiamine assays before and after hydrolysis.

**Table 7-3** Vitamin B1 in Plants*

| No. | Plant Part | Method | Thiamine | TMP | TDP | TTP | References |
|---|---|---|---|---|---|---|---|
| *Aesculus turbinata* Blume (Japanese Horse Chestnut) | | | | | | | |
| 1 | Bud[a] | PC | + | − | ± | + | 3783 |
| *Allium cepa* L. (Onion) | | | | | | | |
| 1 | Bulb[b] | Manom. | | | 120 | | 3684 |
| 1 | Bulb | Manom. | 0.40 | | + | | 3784 |
| *Arachis hypogaea* L. (Peanut) | | | | | | | |
| 1 | Seed cotyledon | PC | + | + | + (ratio 33:10:1) | | 3785 |
| *Avena sativa* L. (Oats) | | | | | | | |
| 2 | Seed | IEC | 3.34-4.48 | 0 | 0 | | 3786 |
| 2 | Seed | Phosphatase | 3.43-4.48 | | 2.08-2.11 | | 3786 |
| 1 | Seed embryo[a] | PC | + | − | ± | + | 3783 |
| 1 | Seedling[c] | Manom. | | | 0.40 | | 3787 |
| *Brassica oleracea* L., ssp. *capitata* L. (Cabbage) | | | | | | | |
| 1 | Leaf, bleached[b] | Manom. | | | 80 | | 3684 |
| *Brassica rapa* L. (Turnip Rape) | | | | | | | |
| 1 | Leaf[b] | Manom. | | | 93 | | 3684 |
| *Camellia japonica* L. (Camellia) | | | | | | | |
| 1 | Pollen[d] | Manom. | | | 57 | | 3430 |

**Table 7-3** Vitamin B1 in Plants*—cont'd

| No. | Plant Part | Method | Thiamine | TMP | TDP | TTP | References |
|---|---|---|---|---|---|---|---|
| *Camellia sasanqua* Thunb. (Sasanqua) | | | | | | | |
| 1 | Pollen[d] | Manom. | | | 51 | | 3430 |
| *Camellia sinensis* L. (Tea) | | | | | | | |
| 1 | Pollen[d] | Manom. | | | 41 | | 3430 |
| *Capsicum annuum* L. (Green Pepper) | | | | | | | |
| 1 | Fruit[b] | Manom. | | | 86 | | 3684 |
| *Carya illinoinensis* (Wang.) K. Koch (Pecan) | | | | | | | |
| 1 | Nut[b] | Manom. | | | 170 | | 3684 |
| *Castanea* spp. (Chestnut) | | | | | | | |
| 1 | Nut | Manom. | 2.83 | | 0.18 | | 3784 |
| *Citrus natsudaidai* Hayata (Sour Orange) | | | | | | | |
| 1 | Seed embryo[a] | PC | − | − | ± | ± | 3783 |
| *Citrus sinensis* (L.) Osbeck (Orange) | | | | | | | |
| 1 | Seed[b] | Manom. | | | 250 | | 3684 |
| 1 | Fruit, juice[b] | Manom. | | | 80 | | 3684 |
| 1 | –, juice | GFC | 0.630 | | 0.764 | | 3729 |
| 1 | –, peel[b] | Manom. | | | 125 | | 3684 |
| *Coffea arabica* L. (Coffee) | | | | | | | |
| 1 | Seed | Phosphatase | 11.68 | | Low | | 3788 |
| *Colocasia esculenta* (L.) Schott. (Taro) | | | | | | | |
| 1 | Leaf | Manom. | 0.90 | | 0.11 | | 3784 |
| *Cucurbita pepo* L. (Pumpkin) | | | | | | | |
| 1 | Germ, axis[a] | PC | − | ± | + | + | 3783 |
| 1 | –, cotyledon[a] | PC | + | − | − | − | 3783 |
| *Cucurbita* spp. (Squash) | | | | | | | |
| 1 | Fruit[b] | Manom. | | | 107 | | 3684 |
| *Cycas revoluta* Thunb. (Sago Palm) | | | | | | | |
| 1 | Seed | HPLC | | | +[e] | | 3775 |
| *Fagopyrum esculentum* Moench (Buckwheat) | | | | | | | |
| 1 | Seed | Manom. | 2.04 | | 1.89 | | 3784 |
| 1 | Whole seedling | PC | − | − | + | + | 3783 |
| *Glycine max* (L.) Merr. (Soybean) | | | | | | | |
| 1 | Seed | Phosphatase | | | 19.1 | | 3789 |
| 1 | Germ, axis | PC | − | − | ± | + | 3783 |
| 1 | –, cotyledon | PC | + | − | + | + | 3783 |
| 1 | Seedling[a] | PC | | | + | − | 3780 |
| 1 | Sprout | Phosphatase | | | 31.8 | | 3789 |
| 1 | Meal | Phosphatase | 4.4 | | 6.6 | | 3790 |
| *Helianthus tuberosus* L. (Jerusalem Artichokie) | | | | | | | |
| 1 | Excised sprout[a] | PC | + | − | ± | + | 3783 |
| *Hordeum vulgare* L. (Barley) | | | | | | | |
| 2 | Seed | IEC | 2.07-2.85 | 0 | 0 | | 3786 |
| 2 | Seed | Phosphatase | 2.16-2.54 | 1.72-1.91 | 563 | | |
| 1 | Seedling[f] | Manom. | | | 0.24 | | 3791 |

*μg/g fresh weight basis, unless stated otherwise; [a]Levels: +, clearly detectable; ±, ambiguous; −, trace or not detectable; [b]μL $CO_2$/g; [c]μg/plant part; [d]Relative to yeast cocarboxylase = 100; [e]Protein binding; [f]mg $CO_2$/g; [g]nmol/g; [h]Dry weight basis.

*Continued*

**Table 7-3** Vitamin B1 in Plants*—cont'd

| No. | Plant Part | Method | Thiamine | TMP | TDP | TTP | References |
|---|---|---|---|---|---|---|---|
| *Larix leptolepis* Gord. (Japanese Larch) | | | | | | | |
| 1 | Bud[a] | PC | – | ± | ± | ± | 3783 |
| *Lilium auratum* Lindl. (Golden-Rayed Lily) | | | | | | | |
| 1 | Pollen[d] | Manom. | | | 39 | | 3430 |
| *Lilium longiflorum* Thunb. (Trumpet Lily) | | | | | | | |
| 1 | Pollen[d] | Manom. | | | 45 | | 3430 |
| *Lilium philippinense* Bak. (Philippine Lily) | | | | | | | |
| 1 | Pollen[d] | Manom. | | | 45 | | 3430 |
| *Lilium* spp. (Lily) | | | | | | | |
| 1 | Bulb | Manom. | 2.34 | | 0.28 | | 3784 |
| *Lycopersicon esculentum* Mill. (Tomato) | | | | | | | |
| 1 | Fruit | Manom. | 0.70 | | + | | 3784 |
| *Oryza sativa* L. (Rice) | | | | | | | |
| 1 | Seed, rough | IEC | 1.53 | 0.0 | 0.053 | 0.017 | 3685 |
| 1 | Seed, embryo[a] | PC | + | – | ± | + | 3783 |
| 1 | –, endosperm[a] | PC | + | – | – | – | 3783 |
| 1 | Seed, unmilled | Manom. | 2.70 | | 1.15 | | 3784 |
| 1 | Polish | Phosphatase | 203 | | 42 | | 3792 |
| 1 | Germ | IEC | 36.00 | 0.0 | 0 | | 3685 |
| 1 | Bran | IEC | 2.440 | 0.0 | 0.0 | 0.0 | 3685 |
| *Paeonia albiflora* Pall. (Chinese Peony) | | | | | | | |
| 1 | Pollen[d] | Manom. | | | 33 | | 3430 |
| *Papaver orientale* L. (Oriental Poppy) | | | | | | | |
| 1 | Pollen[d] | Manom. | | | 15 | | 3430 |
| *Papaver somniferum* L. (Opium Poppy) | | | | | | | |
| 1 | Pollen[d] | Manom. | | | 53 | | 3430 |
| *Persea americana* Mill. (Avocado) | | | | | | | |
| 1 | Fruit | Phosphatase | | | 1.046 | | 3793 |
| *Pharbitis nil* (L). Choisy (Morning Glory) | | | | | | | |
| 1 | Seed embryo[a] | PC | – | – | ± | ± | 3783 |
| *Phaseolus vulgaris* L. (String Beans) | | | | | | | |
| 1 | Bean | Manom. | 2.08 | | 0.11 | | 3784 |
| 1 | Bean, cotyledon | Phosphatase | 3.45 | | 0.72 | | 3794 |
| 1 | –, seed coat | Phosphatase | 0.53 | | 0.20 | | 3794 |
| 1 | –, decotylized embryo | Phosphatase | 12.52 | | 0.96 | | 3794 |
| 1 | –, first leaf | Phosphatase | 6.17 | | 2.56 | | 3794 |
| 1 | –, hypocotyl | Phosphatase | 9.51 | | 0.94 | | 3794 |
| 1 | –, transitional region | Phosphatase | 26.15 | | 4.01 | | 3794 |
| 1 | –, radicle | Phosphatase | 36.13 | | 9.93 | | 3794 |
| *Picea abies* (L.) Karst. (Spruce) | | | | | | | |
| 1 | Seed | HPLC | | | +[e] | | 3775 |
| *Pinus densiflora* Sieb. and Zucc. (Japanese Red Pine) | | | | | | | |
| 1 | Whole seedling[a] | PC | + | – | ± | + | 3783 |
| 1 | Pollen[d] | Manom. | | | 6 | | 3430 |
| *Pisum sativum* L. (Peas) | | | | | | | |
| 1 | Seed | Phosphatase | 1.0 | | 1.0 | | 3780 |

**Table 7-3** Vitamin B1 in Plants*—cont'd

| No. | Plant Part | Method | Thiamine | TMP | TDP | TTP | References |
|---|---|---|---|---|---|---|---|
| 1 | Germ, axis | Phosphatase | 0 | | 3.25 | | 3780 |
| 1 | Germ, axis[a] | PC | − | − | ± | + | 3783 |
| 1 | –, cotyledon[a] | PC | + | − | + | + | 3783 |
| 1 | Seedling[a] | PC | | | − | + | 3780 |
| 1 | Seedling | Phosphatase | 57.3 | | 23.4 | | 3795 |
| 1 | Stem and leaf | Phosphatase | 25.4 | | 11.4 | | 3795 |
| *Platanus occidentalis* L. (Eastern Sycamore) | | | | | | | |
| 1 | Bud[a] | PC | − | − | ± | ± | 3783 |
| *Prunus armeniaca* L. (Apricot) | | | | | | | |
| 1 | Fruit | Teysseire | 0.60 | | 0 | | 3779 |
| *Prunus dulcis* (Mill.) D. A. Webb (Almond) | | | | | | | |
| 1 | Seed, shelled[g] | HPLC | 5.1 | 0.35 | 0.29 | | 3781 |
| *Pseudosasa japonica* Mak. (Arrow Bamboo) | | | | | | | |
| 1 | Bud[a] | PC | + | + | + | + | 3783 |
| *Pyrus communis* L. (Pear) | | | | | | | |
| 1 | Fruit | Phosphatase | | | 0.703 | | 3793 |
| *Raphanus sativus* L. (Radish) | | | | | | | |
| 1 | Whole seedling[a] | PC | + | − | + | + | 3783 |
| *Sagittaria sagittifolia* L. (Arrowhead) | | | | | | | |
| 1 | Seed | Phosphatase | 0.84 | | 0.40 | | 3784 |
| *Solanum tuberosum* L. (Potato) | | | | | | | |
| 1 | Tuber | Phosphatase | 0.55 | | + | | 3784 |
| *Spinacia oleracea* L. (Spinach) | | | | | | | |
| 1 | Seed | HPLC | | | +[c] | | 3775 |
| 1 | Leaf[b] | Manom. | | | 10 | | 3684 |
| 1 | Leaf | Manom. | 1.30 | | + | | 3784 |
| *Triticum aestivum* L. (Wheat) | | | | | | | |
| 2 | Grain | Phosphatase | 1.28-1.65 | | 1.61-2.42 | | 3786 |
| 2 | Grain | IEC | 1.16-1.68 | 0 | 0 | | 3786 |
| 1 | Grain | Teysseire | 1.00 | | 0 | | 3779 |
| 75 | Flour | Phosphatase | 1.6-7.5 | | 0 | | 3796 |
| 1 | Flour | GFC | 0.222 | | 0 | | 3729 |
| 1 | Seed, embryo[a] | PC | + | − | + | + | 3783 |
| 1 | –, endosperm[a] | PC | + | − | − | − | 3783 |
| 1 | Germ | Phosphatase | 20-25 | | 0.5 | | 3797 |
| 1 | Germ | IEC | 4.56 | 0.0 | 0.33 | 0.0 | 3685 |
| 1 | Bran | Teysseire | 4.50 | | 0 | | 3779 |
| 1 | Seedling | Teysseire | 1.00 | | 0.50 | | 3779 |
| 1 | Seedling | Phosphatase | 3.7 | | 3.7 | | 3798 |
| *Vitis coignetiae* Pull. (Crimson Glory Vine) | | | | | | | |
| 1 | Bud[a] | PC | − | − | − | ± | 3783 |
| *Xanthium strumarium* L. (Cocklebur) | | | | | | | |
| 1 | Seed embryo[a] | PC | + | + | + | + | 3783 |

*μg/g fresh weight basis, unless stated otherwise; [a]Levels: +, clearly detectable; ±, ambiguous; −, trace or not detectable; [b]μL $CO_2$/g; [c]μg/plant part; [d]Relative to yeast cocarboxylase = 100; [e]Protein binding; [f]mg $CO_2$/g; [g]nmol/g; [h]Dry weight basis.

*Continued*

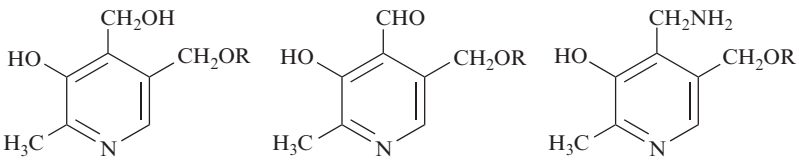
**Table 7-3** Vitamin B1 in Plants*—cont'd

| No. | Plant Part | Method | Thiamine | TMP | TDP | TTP | References |
|---|---|---|---|---|---|---|---|
| *Zea mays* L. (Corn) | | | | | | | |
| 1 | Seed | PC | | | − | − | 3780 |
| 1 | Seed | HPLC | | | +[e] | + | 3775 |
| 1 | –, embryo[a] | PC | + | − | ± | + | 3783 |
| 1 | Seedling[a] | PC | | | − | + | 3780 |
| Vegetables | | | | | | | |
| 1 | Edible parts[b] | − | | + | + | + | 3799 |
| Collected by honey bees from various floral sources | | | | | | | |
| 1 | Pollen[g,h] | HPLC | 11-40 | 1-6 | 1-13 | | 3800 |

*μg/g fresh weight basis, unless stated otherwise.
[a]Levels: +, clearly detectable; ±, ambiguous; −, trace or not detectable.
[b]μL $CO_2$/g.
[c]μg/plant part.
[d]Relative to yeast cocarboxylase = 100.
[e]Protein binding.
[f]mg $CO_2$/g.
[g]nmol/g.
[h]Dry weight basis.

# Vitamin $B_6$

The vitamin $B_6$ complex comprises pyridoxine (PN, also called pyridoxol), pyridoxal (PL), and pyridoxamine (PM), together with the monophosphate esters pyridoxal 5′-phosphate (PLP, codecarboxylase) and pyridoxamine 5′-phosphate (PMP). The missing member of this group, pyridoxine 5′-phosphate (PNP), has no vitamin $B_6$ activity.




**PN**, R = H
**PNP**, R = $P(O)(OH)_2$

**PL**, R = H
**PLP**, R = $P(O)(OH)_2$

**PM**, R = H
**PMP**, R = $P(O)(OH)_2$

Pyridoxine 5′-Phosphate (PNP), $C_8H_{12}NO_6P$ [R.N. 447-05-2]; Beilstein **21** III/IV 2516. *3,4-Pyridinedimethanol, 5-Hydroxy-6-methyl-, $\alpha^3$-(Dihydrogen Phosphate)*.

Pyridoxal 5′-Phosphate (PLP), $C_8H_{10}NO_6P$ [R.N. 54-47-7]; Beilstein **21** IV 6420. *4-Pyridinecarboxaldehyde, 3-Hydroxy-2-methyl-5-[(phosphonooxy)methyl]-*.

Pyridoxamine 5′-Phosphate (PMP), $C_8H_{13}N_2O_5P$ [R.N. 529-96-4]; Beilstein **22** IV 6065. *3-Pyridinemethanol, 4-(Aminomethyl)-5-hydroxy-6-methyl-, α-(Dihydrogen Phosphate)*.

## Occurrence

Pyridoxal 5′-phosphate (PLP) was first identified in peas and cabbage by Gale and Epps[3802] in 1944, pyridoxamine 5′-phosphate (PMP) in Cerophyl, a grass product, by Rabinowitz and Snell[3803] in 1947, and pyridoxine 5′-phosphate (PNP) in rice bran by Yasumoto *et al.*[3804] in 1976. PLP is a component of potato phosphorylase [E.C. 2.4.1.1], which contains one PLP group per subunit.[3805] Removal of the PLP by incubation with acidic hydroxylamine leaves the apoenzyme catalytically inactive.[3806] It is also a component of other plant enzymes such as those of peas (starch phosphorylase, E.C. 2.4.1.1),[3807] blue lupine (β-cyanoalanine synthetase, E.C. 4.4.1.9, one mol PLP/mol),[3808] rape leaf (cysteine synthetase, E.C. 4.2.99.8, two mols PLP per mol),[3809] *Acacia farnesiana* seedling (*S*-alkyl-L-cysteine lyase, E.C. 4.4.1.6, one mol PLP per mol),[3810] and grass pea seedling (arginine decarboxylase, E.C. 4.1.1.19).[3811] More recent studies show that PNP occurs to some extent in the form of glucosides.[3804,3812]

The metabolic pathways for the biosynthesis of the $B_6$ vitamins in plants are unknown, but they may be identical to those for microbial organisms such as *Escherichia coli*, which are outlined in Fig. 7-2. In step 1, PNP is formed by the coupling of 1-deoxy-D-xylulose 5-phosphate (**3**, dXu5P) and 4-hydroxy-1-threonine 4-phosphate (**4**)[3813]; dXu5P is also an intermediate in the biosynthesis of TDP (Fig. 7-1). In step 2, PNP is oxidized to PLP, and in step 3, PLP undergoes reversible transamination giving PMP. All three vitamin $B_6$ phosphates are hydrolyzed to the phosphate-free forms by phosphatase (step 4), and all three of the latter are phosphorylated by ATP in the presence of the same enzyme, pyridoxal kinase (step 5).

## Physical Properties

### Pyridoxine 5′-Phosphate

PNP [R.N. 447-05-2]: White needles, mp 208-210 °C,[3814] soluble in water, insoluble in alcohol and ether; p$K_a$ (potentiometric and UV).[3815] Spectra: UV,[3816] luminescence,[3817] $^1$H NMR (fig.).[3778] Chromatography: PC,[3816] TLC,[41] IEC,[3816,3818] HPLC,[3819] GC,[3820] Sephadex gel.[3821] Electrophoresis: paper,[3822] thin layer,[41,3823] HPCE.[3824]

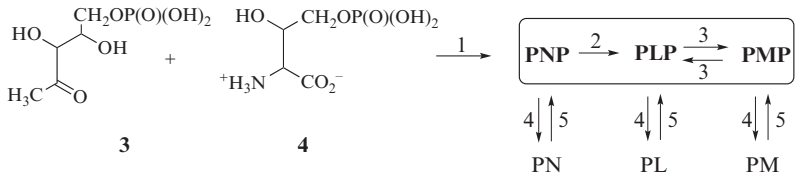



**FIGURE 7-2** Vitamin $B_6$ Phosphates. (1) PNP synthase. (2) Pyridoxine 4-dehydrogenase [E.C. 1.1.1.65], NADP. (3) PMP oxidase [E.C. 1.4.3.5], FMN, $O_2$, $H_2O$. (4) Phosphatase [E.C. 3.1.3.2]. (5) Pyridoxal kinase [E.C. 2.7.1.35], ATP.

### Pyridoxal 5′-Phosphate

PLP·$H_2O$ [R.N. 54-47-7]: Microscopic lemon-yellow needles[3825] (photo[3826]); mp 139-143 °C dec. or 143 °C reported for the commercial product[3827,3828]; hardly soluble in water, methanol, ethanol, and acetone; insoluble in ether, chloroform, and benzene, but easily soluble in formic acid and DMF[3826]; sensitive to light.[3814] p$K_a$: potentiometric,[3829] NMR.[3830,3831] Spectra: IR[3829] (fig.[3832]), UV,[3833,3834] fluorescence,[3835] phosphorescence,[3836] $^1$H NMR (fig.),[3837] $^{13}$C NMR,[3831,3838] $^{31}$P NMR,[3830] MS (field desorption).[3839] X-Ray structure.[3840] Chromatography: PC,[3816] TLC[41,3841] (two-dimensional[3842]), IEC (resin,[3818] cellulose[3841]), HPLC,[3819,3843] GC,[3820] Sephadex gel.[3157] Electrophoresis: paper,[32,3844] starch column,[3844] thin layer,[41,3823] HPCE.[3824] Polarographic reduction.[3828,3845]

$CaC_8H_8NO_6P·3H_2O$ [R.N. 5913-70-2]: Lemon-yellow powder, slightly soluble in water.[3846]

$BaC_8H_8NO_6P·3H_2O$: Yellow solid, soluble in water and ethanol, insoluble in ether.[3847]

$C_{13}H_9N$·PLP·$H_2O$ (acridine salt): Fine lemon-yellow needles, readily soluble in water and ethanol, insoluble in ether.[3847]

### Pyridoxamine 5′-Phosphate

PMP [R.N. 529-96-4]: Fine, very hygroscopic needles.[3848]

PMP·$2H_2O$: White rods (photo)[3826] or rhombic plates[3848]; hardly soluble in water, alcohol, and pyridine and insoluble in ether, chloroform, and benzene[3826]; photosensitive.[3849] p$K_a$: potentiometric,[3850] NMR.[3830,3848] Spectra: UV,[3816,3850] fluorescence,[3849,3851] phosphorescence,[3852] $^1$H NMR (fig.),[3837] $^{13}$C NMR,[3831,3838] $^{31}$P NMR,[3830] MS (field desorption).[3839] Chromatography: PC,[3816] TLC[41,3841] (two-dimensional[3842]), IEC (resin,[3818] cellulose[3841]), HPLC,[3819,3843] Sephadex gel.[3157] Electrophoresis: paper,[32,3844] thin layer,[41,3823] starch column,[3844] HPCE.[3824] Polarographic reduction.[3828]

PMP·HCl·$H_2O$: Colorless crystals, mp 222-224 °C dec.[3853]; IR (fig.)[3832]; X-ray structure.[3854]

$CaC_8H_{11}N_2O_5P·4H_2O$: Solid. UV.[3853]

## Synthesis

Pyridoxine 5′-phosphate (PNP) may be prepared (a) by phosphorylation of pyridoxine with phosphorus oxychloride[3833] or phosphoric acid-phosphorus pentoxide,[3822] (b) by phosphorylation of isopropylidenepyridoxine with phosphoric acid-phosphorus pentoxide[3826] or 2-cyanoethyl phosphate,[3778] (c) by reduction of PLP with sodium borohydride,[3814,3815] (d) by deamination of PMP with sodium nitrite,[3816] or (e) by oxidation of pyridoxine 5′-phosphite with potassium permanganate.[3855]

Pyridoxal 5′-phosphate (PLP) may be prepared (a) by oxidation of PNP[3833,3856] or PMP[3825] with manganese dioxide, (b) by transamination of PMP with pyruvic acid in the presence of a Cu(II) salt,[3857] or (c) by phosphorylation of an aldehyde-protected PLP with phosphoric acid-phosphorus pentoxide, polyphosphoric acid, or

metaphosphoric acid, followed by removal of the protecting group (hydrazone,[3846] oxime, Schiff base,[3858,3859] enamine,[3860] acetal, and the like). Phosphorylation of pyridoxal with phosphorus oxychloride gives poor yields of PLP even when the aldehyde group is protected.[3833]

Pyridoxamine 5′-phosphate (PMP) may be prepared (a) by transamination of PLP with glutamic acid[3803] or (b) by phosphorylation of pyridoxamine with phosphoric acid-phosphorus pentoxide,[3848] metaphosphoric acid,[3853] or (in low yield) phosphorus oxychloride.[3861] The initial product of phosphorylation with metaphosphoric acid is the 5′-triphosphate, which yields PMP upon hydrolysis at 100 °C with water (2 h) or 1*N* HCl (10 min).[3853]

## Hydrolysis

PMP is more resistant to hydrolysis than PNP or PLP. Less than 0.4% of its phosphorus was detected as $P_i$ after 54 days' storage in aqueous solution at 7 °C, compared to 2.6% for PNP and 2.1% for PLP. Hydrolysis with 1*N* HCl at 100 °C for 15.3 h gave 23% $P_i$ compared to 35% for PNP and 73% for PLP; hydrolysis with 1*N* NaOH under the same conditions, however, gave 10% $P_i$ versus 11% (0%[3815]) for PNP and 6% for PLP. Complete hydrolysis was achieved with 6*N* $H_2SO_4$ after 55 h (30 h for PLP) at 100 °C.[3816]

The hydrolysis of PLP is catalyzed by acids[3816] and metal ions.[3678] Unlike most other phosphate esters, PLP is most stable at pH 2; the first-order rate constant $K_D$ is $1.9 \times 10^{-4}$ (pH 1.92, 87 °C)[3862] or $3.96 \times 10^{-4}$ (pH 2.05, 98 °C).[3827]

The phosphate groups were cleaved during the preparation of 5′-deoxypyridoxine and 5′-deoxypyridoxamine from PLP and PMP by catalytic hydrogenolysis with Pd/C[3863,3864] but not from PLP with sodium borohydride.[3814,3815]

## Complex Formation

Bivalent and trivalent metal ions such as Cu(II), Zn(II), or Dy(III) react with PLP and PMP forming 1:1 complexes that are insoluble, intractable, and probably polymeric.[3832,3865] Such complexes are important in relation to the metal ion catalysis of transamination reactions between the vitamin $B_6$ compounds and amino acids *in vitro* and *in vivo*.

## Extraction, Separation, and Analysis

### *(1) Ion Exchange chromatography (IEC) Method*

de Obieta and Munoz[3866] used this method to separate the vitamin $B_6$ components of germinating *Pinus pinea* seeds, using the azine method of Soda *et al.*[3867] to assay for PLP.

### *(2) High-Performance Liquid Chromatography (HPLC) Method*

This method is now the method of choice for the analysis of the $B_s$ vitamins because they can be separated and quantitated in a single run, usually carried out in the reversed-phase mode with HPLC column packings such as μ-Bondapak $C_{18}$[3868] or TSK gel

ODS-120A,[3869,3870] or, in one instance, in the ion-pairing mode with Beckman Ultrasphere IP.[3871] The following procedure is typical:

> *Solid samples (2 g) were mixed with 9 mL of 5 % (w/v) SSA [sulfosalicylic acid] and 1 mL of a solution of 4-dPN [4′-deoxypyridine] (typically 120 nmol/mL in 5 % SSA) and then homogenized with a Polytron homogenizer . . . for 45 s . . . Ten milliliters of methylene chloride was added, and the mixture was blended for 20 s . . . The homogenates were centrifuged at 9000 g for 15 min. at 2° C, after which an aliquot of the aqueous layer was removed . . . . Preparative anion-exchange chromatography was performed [on the aliquot] with a column packed with Bio-Rad AG2-X8 . . . to remove SSA and purify the sample extracts. The biologically active $B_6$ vitamers, 4-dPN, and PN-glucoside eluted as a single fluorescing peak near the void volume (retention time approximately 4 min). The eluate either was analyzed directly or was subjected to enzymatic hydrolysis prior to HPLC analysis . . . . The HPLC analytical system . . . consisted of two solvent metering pumps, [a gradient controller, injection valve, and a fluorometric detector]. Fluorometric detection was enhanced by using the postcolumn phosphate-bisulfite reagent . . . . The separation was performed at ambient temperature by using a linear gradient . . . from 100 % solvent A1 [0.033*M *K phosphate and 8 m*M *octanesulfonic acid, pH 2.2] to 100 % solvent A2 [solvent A1 + 2.5 % (v/v) 2-propanol, pH 2.2] in 12 min., followed by a programmed switch to 100 % solvent B [0.033*M *K phosphate and 6.5 % 2-propanol, pH 2.2] 15 min after injection . . . . Quantitation was done relative to the response of the internal standard 4′-deoxypyridine.*
>
> Reprinted with permission from Gregory, J. F., III; Ink, S. L. J., "Identification and Quantification of Pyridoxine β-Glucoside as a Major Form of Vitamin $B_6$ in Plant-Derived Foods", *J. Agric. Food Chem.* **1987**, *35*(1), 76–82,[3872] © 1987 American Chemical Society.

### *(3) Enzymatic Methods*

#### (A) TRYPTOPHANASE METHOD

In this method, PLP is assayed with the apoenzyme of *E. coli* tryptophanase [E.C. 4.1.99.1], the amount of indole produced from added tryptophan being measured colorimetrically by Ehrlich's aldehyde reaction. The apoenzyme of Baker's yeast or pig heart aspartate aminotransferase [E.C. 2.6.1.1] proved to be unsuitable for this purpose.[3873]

> *A weighed sample of plant tissue (100 mg) was dissolved in the cold in a porcelain mortar or glass blender with 0.3 ml of freshly prepared 5 % $HPO_3$; 2.6 ml of distilled water was added to the mixture, and after supplementary grinding of the tissue, the mixture was heated for 5 min at 80°. Then the mixture was chilled, centrifuged, and the supernatant liquid used to determine PALP. No more than 0.3 ml of the $HPO_3$ extract of the plant tissue was taken for analysis . . . . All the work associated with the production of $HPO_3$ extracts of plant tissue, with the exception of the stage of*

*heating, was conducted at 0-4°, the tissue shielded from the action of bright light. The PALP content was determined in the extracts . . . 1 h after their preparation.*

Zavenyagina, T. N.; Bukin, Yu. V., "Content of Pyridoxal 5-Phosphate in Wheat and Pea Seed and Seedlings", *Biokhimiya* **1971**, *36*(1), 205–215 [Engl. 172–180],[3873] reprinted by permission of the Editor-in-Chief, Biochemistry (Moscow)/Biokhimiya, © 1971.

**(B) PHOSPHATASE METHOD**

Yasumoto *et al.*[3804] determined the vitamin $B_6$ content of cereals and other seeds by microbial assay with *Saccharomyces carlsbergensis* following hydrolysis with either takadiastase or acid. In most cases, digestion with takadiastase was sufficient, but part of the pyridoxine in rice bran, kaoliang, and trefoil was bound in a takadiastase-resistant form. In rice bran, about 4 μg/g of the bound pyridoxine was identified as pyridoxine β-glucoside and about 1 μg/g as PNP.

### *(4) Fluorometric Method*

Zavenyagina and Bukin[3873] described a method in which the PLP content of peas and wheat was determined after oxidation to pyridoxa-4,5-lactone, a highly fluorescent substance, in the presence of oxygen in slightly alkaline solution. The protein-free extracts (pH 7.4) were incubated with KCN for 2.5 h at 25 °C, acidified to pH 3.5 with glacial acetic acid, and the fluorescence intensity measured at 420 nm with extinction at 313 nm. The results were comparable to those of the tryptophanase method.[3873]

**Table 7-4** Vitamin $B_6$ Content of Plants*

| No. | Plant part | Method | PNP | PLP | PMP | Total $B_6$ | References |
|---|---|---|---|---|---|---|---|
| *Asparagus officinalis* L. (Asparagus) | | | | | | | |
| 1 | Stem | HPLC | | | 0.144 | 0.183 | 3869 |
| *Avena sativa* L. (Oats) | | | | | | | |
| 1 | Bran | HPLC | | 0.707 | 0 | 1.15 | 3871 |
| *Brassica oleracea* L. ssp. *capitata* L. (Cabbage) | | | | | | | |
| 1 | Juice[a] | HPLC | 0.03 | 0.27 | 0.05 | 1.21 | 3870 |
| *Brassica oleracea* L. ssp. *italica* Plenck. (Broccoli) | | | | | | | |
| 1 | Raw head | HPLC | | 1.44 | 0.41 | 2.71 | 3872 |
| 1 | Head | HPLC | 0.11 | 1.15 | 0.38 | 2.73 | 3870 |
| *Citrus sinensis* (L.) Osbeck (Orange) | | | | | | | |
| 1 | Fruit juice[a] | HPLC | | n.d. | 0.26 | 1.47 | 3872 |
| 1 | Fruit juice[a] | HPLC | 0.021 | 0.051 | 0.028 | 0.199 | 3869 |
| *Daucus carota* L. (Carrot) | | | | | | | |
| 1 | Root | HPLC | | 0.53 | 0.18 | 4.42 | 3872 |
| 1 | Root | HPLC | + | + | | + | 3812 |
| *Glycine max* (L.) Merr. | | | | | | | |
| 1 | Flour | HPLC | | 0 | 0 | 5.13 | 3871 |

*Continued*

**Table 7-4** Vitamin $B_6$ Content of Plants*—cont'd

| No. | Plant part | Method | PNP | PLP | PMP | Total $B_6$ | References |
|---|---|---|---|---|---|---|---|
| *Helianthus tuberosus* L. (Sunflower) | | | | | | | |
| 1 | Seed | HPLC | + | + | | + | 3812 |
| 1 | Sprout | HPLC | + | + | | + | 3812 |
| *Malus domestica* Borkh. (Apple) | | | | | | | |
| 1 | Fruit juice[a] | HPLC | | 0.018 | 0.006 | 0.074 | 3869 |
| *Medicago sativa* L. (Alfalfa) | | | | | | | |
| 1 | Sprout | HPLC | | 0.48 | 0.45 | 8.10 | 3872 |
| *Musa paradisiaca* L. (Banana) | | | | | | | |
| 1 | Fruit | HPLC | | 0.79 | 0.07 | 3.65 | 3872 |
| 1 | Fruit | HPLC | 0.022 | 1.29 | 0.040 | 3.273 | 3869 |
| *Oryza sativa* L. (Rice) | | | | | | | |
| 1 | Bran | HPLC | 0.097 | | | 2.107 | 3869 |
| 1 | Bran | HPLC | | 1.80 | 0 | 12.10 | 3871 |
| 1 | Bran | Enzym. | 16.0 | <0.5 | <0.5 | 19.5 | 3804 |
| *Pennisetum* spp. | | | | | | | |
| 1 | Seed | HPLC | + | + | | + | 3812 |
| *Phaseolus lunatus* L. (Lima Bean) | | | | | | | |
| 1 | Bean | HPLC | | 5.61 | 0.22 | 6.99 | 3868 |
| *Phaseolus vulgaris* L. (Bean) | | | | | | | |
| 1 | Bean, raw green | HPLC | | 1.03 | 0.31 | 2.69 | 3872 |
| *Pinus pinea* L. (Italian Stone Pine) | | | | | | | |
| 1 | Seed, embryo | IEC | | 42.0 | | 11.9 | 3866 |
| 1 | –, endosperm | IEC | | 107.6 | | 1.1 | 3866 |
| *Pisum sativum* L. (Peas) | | | | | | | |
| 1 | Whole seed[b] | Enzym. | | 0.17 | | | 3873 |
| 1 | Seedling, leaf[b] | Enzym. | | 1.39 | | | 3873 |
| 1 | –, root[b] | Enzym. | | 0.25 | | | 3873 |
| 1 | Leaf | Fluor. | | + | | | 3873 |
| Seaweed | | | | | | | |
| 1 | –[c] | HPLC | + | + | | + | 3874 |
| *Secale cereale* L. (Rye) | | | | | | | |
| 1 | Seed | HPLC | + | + | | + | 3812 |
| *Solanum tuberosum* L. (Potato) | | | | | | | |
| 1 | Tuber | HPLC | | 1.09 | | 12.05 | 3875 |
| *Triticum aestivum* L. (Wheat) | | | | | | | |
| 1 | Whole seed[b] | Enzym. | | 0.19 | | | 3873 |
| 1 | Whole seed | Fluor. | | + | | | 3873 |
| 1 | Sprout, leaf[b] | Fluor. and variation in PLP content from base to tip | | + | | | 3873 |
| 1 | –, leaf | Fluor. | | + | | | 3873 |
| 1 | –, root | Fluor. | | + | | | 3873 |
| 1 | –, root[b] | Enzym. | | 0.32 | | | 3873 |
| 1 | Seed | HPLC | + | + | | + | 3812 |
| 1 | Whole flour | IEC | | 0.26 | 0.27 | 4.30 | 3876 |
| 1 | Flour | HPLC | 0.031 | 0.18 | 0.022 | 0.289 | 3869 |
| 1 | Bran | HPLC | | | 0 | 7.93 | 3871 |

*µg/g fresh weight basis, unless stated otherwise.
[a]µg/mL.
[b]Dry weight basis.
[c]Not given in the abstract.

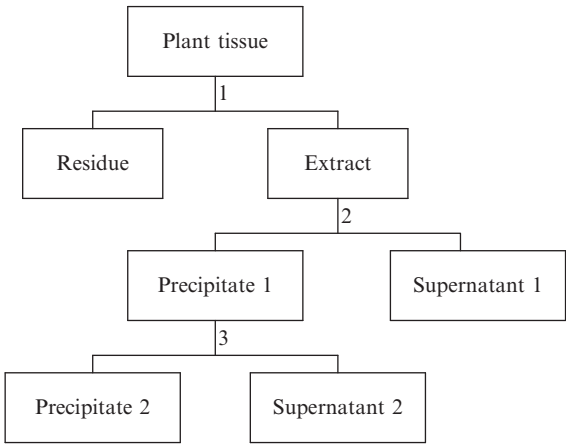
# 8 Distribution of Phosphorus Compounds in Plants

This chapter describes early efforts to develop a comprehensive fractionation scheme for determining the relative amounts of the major classes of phosphorus-containing compounds—lipids, sugars, phytic acid, nucleotides, nucleic acids, proteins, and $P_i$—in plants that would hopefully enable a balance sheet to be drawn up. Many such schemes have been proposed but few have achieved even limited acceptance. The earliest efforts were those of Ivanoff,[3877] tribution of $P_i$, $P_{lipid}$, $P_{nucl}$, and $P_{protein}$ in germinating vetch,[3877] rice,[3878] and chickpea,[3879] respectively. The culmination of these efforts appears in the last table of this chapter in which a balance sheet is drawn up for the distribution of individual phosphorus compounds in a single plant species, duckweed (*Spirodela oligorrhiza*), using modern methods of analysis.[327]

The principal methods can be broadly separated into four categories: selective precipitation methods, selective extraction methods, chromatographic methods, and $^{31}P$ NMR methods.

## Selective Precipitation Methods

In the LePage and Umbreit method (Scheme 8-1), which focuses on the acid-soluble components, the plant tissue is extracted exhaustively with 10% trichloroacetic acid (TCA), and the extract is separated by fractional precipitation into three fractions: a




**SCHEME 8-1 LePage and Umbreit Method**. Reagents: (1) 10% TCA. (2) 50% KOH, $Ba(OAc)_2$, EtOH. (3) 2*N* HCl, Ba $(OAc)_2$, $H_2SO_4$.


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**Table 8-1** Selective Precipitation Methods*

| No. | Plant part | $P_i$ | $P_{lipid}$ | $P_{sugar}$ | $P_{phytate}$ | $P_{nucleotide.}$ | $P_{protein}$ | $P_{total}$ | References |
|---|---|---|---|---|---|---|---|---|---|
| | | | | **LePage and Umbreit Method** | | | | | |
| *Avena sativa* L. (Oats) | | | | | | | | | |
| 1 | Seed embryo | 34.2 | | 8.7 | 0.69 | 10.2 | | 5.240[a] | 14 |
| *Beta vulgaris* L. (Sugar Beet) | | | | | | | | | |
| 1 | Leaf | | 7.6 | | 5.3 | | | 0.091 | 15 |
| 1 | Root | | 5.9 | | 5.1 | | | 0.057 | 15 |
| *Lycopersicum esculentum* Mill. (Tomato) | | | | | | | | | |
| 1 | Flower ovary | 30.2 | | 10.0 | | 49.8 | | 1.060 | 18 |
| *Oryza sativa* L. (Rice) | | | | | | | | | |
| 1 | Grain | Change during maturation 3-46 daf | | | | | | | 3882 |
| *Solanum tuberosum* L. (Potato) | | | | | | | | | |
| 2 | Tuber | | | 31 | 68 | | | 0.063 | 315 |
| | | | | **Klein Method** | | | | | |
| *Gossypium hirsutum* L. (Cotton) | | | | | | | | | |
| 1 | Leaf | 50.8 | 0 | 18.5 | | 18.5 | 12.3 | 1.30 | 3883 |
| 1 | Ovule, 10 days | 48.1 | 10.0 | 23.8 | | 14.0 | 4.0 | 0.420 | 3883 |
| 1 | Seed kernel | 8.6 | 8.9 | | 74.9 | 5.0 | 2.7 | 0.935 | 3883 |
| *Lycopersicon esculentum* Mill. (Tomato) | | | | | | | | | |
| 1 | Seedling hypocotyl | 19.5 | 8.5 | | | 23.8 | 6.8 | 0.411 | 3881 |
| | | | | **Other Methods** | | | | | |
| *Cucurbita pepo* L. (Pumpkin) | | | | | | | | | |
| 1 | Leaf mitochondria | 49.5 | 18.2 | 9.0 | | 23.2 | | 0.276 | 1633 |
| *Hordeum vulgare* L. (Barley) | | | | | | | | | |
| 1 | Seed | 5.8 | 11.1 | 10.3 | 60.0 | 12.8 | 0.2 | 0.253 | 996 |
| 1 | –, flour and change on germination 0-6 days[3885] and ripening 19-48 dap[996] | | 3.8 | | | 89.1 | 2.9 | 0.37 | 3884 |
| *Linum usitatissimum* L. (Flax) | | | | | | | | | |
| 1 | Sprout, 7 days | 49.4 | | 19.1 | 7.7 | | | 0.994 | 3886 |
| 1 | Root | 61.8 | | 17.7 | 0 | | | 0.902 | 3886 |
| *Lupinus luteus* L. (Yellow Lupine) | | | | | | | | | |
| 1 | Whole plant | 88.3 | 4.0 | | | 4.8 | | 0.516 | 791 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Oryza sativa* L. (Rice) | | | | | | | | | |
| 1 | Leaf (straw) | 54.0 | 8.1 | | 2.7 | 35.1 | | 0.74 | 1052 |
| 1 | Seed | 5.9 | 8.3 | | 2.8 | 83.0 | | 5.84 | 1052 |
| 1 | –, aleurone particle | 1.7 | 0.1 | | 83.6 | 0.3 | | 11.61 | 1047 |
| | and data for growth from germination to maturity[1052] | | | | | | | | |
| *Petroselinum crispum* (Mill.) A.W. Hill (Parsley) | | | | | | | | | |
| 1 | Leaf | 59.2 | 16.1 | | | 24.7 | | 1.571 | 792 |
| 1 | Root | 64.9 | 13.0 | | | 22.1 | | 1.043 | 792 |
| | and change during growth, August 4 to November 11[792] | | | | | | | | |
| *Secale cereale* L. (Rye) | | | | | | | | | |
| 1 | Seed | 6.3 | 9.6 | 10.2 | 60.5 | 12.0 | 0.2 | 0.342 | 996 |
| | and change on germination 0-6 days[3885] and ripening 19-48 dap[996] | | | | | | | | |
| *Trifolium pratense* L. (Red Clover) | | | | | | | | | |
| 1 | | 76.7 | 7.2 | | 0 | 16.0 | | 0.223 | 791 |
| *Triticum aestivum* L. (Wheat) | | | | | | | | | |
| 1 | Seed | 4.6 | 9.1 | 8.8 | 67.2 | 11.3 | 0.1 | 0.331 | 996 |
| 1 | Seed, ripe | 10.1 | 5.0 | 6.8 | 57.9 | 20.2 | | 0.73 | 3887 |
| 8 | –, flour | 5.3-15.1 | 11.6-13.1 | | 26.3-42.6 | 12.4-17.4 | | 0.092-0.140 | 759 |
| | and change on germination 0-6 days[3885] and change on ripening 19-48 dap[996] or 0-36 daf[3887] | | | | | | | | |
| *Triticum durum* Desf. (Durum Wheat) | | | | | | | | | |
| 2 | Seed flour | 5.1-5.5 | 11.9-12.9 | | 31.7-38.1 | 17.6-22.3 | | 0.112-0.125 | 759 |
| *Zea mays* L. (Corn) | | | | | | | | | |
| 1 | Seed flour | 12.9 | 4.1 | | 75.5 | 11.5 | | 0.349 | 791 |
| 1 | Root | 52.5 | 0.44 | 15.7 | | 31.3 | | | 3888 |
| | and change during growth, August 2 to October 30[791] | | | | | | | | |

*$P_{total}$ column: Percent P by weight of plant tissue, fresh weight basis. Other columns: Percent of $P_{total}$.
[a]mg/100 embryos.

barium-insoluble fraction (precipitate 2) containing PGA, F1,6P, ATP, phytic acid, and $P_i$; a barium-soluble fraction (supernatant 2) containing the hexose monophosphates (G1P, G6P, F6P), PEP, and TP; and an ethanol-soluble fraction (supernatant 1) containing unidentified phosphorus compounds. The components of each fraction are identified by their characteristic properties.[3] When this method is applied to animal or bacterial tissue, it is possible to draw up a balance sheet that accounts for over 90% of the compounds present, but the method is not as successful when applied to plant tissue.[14]

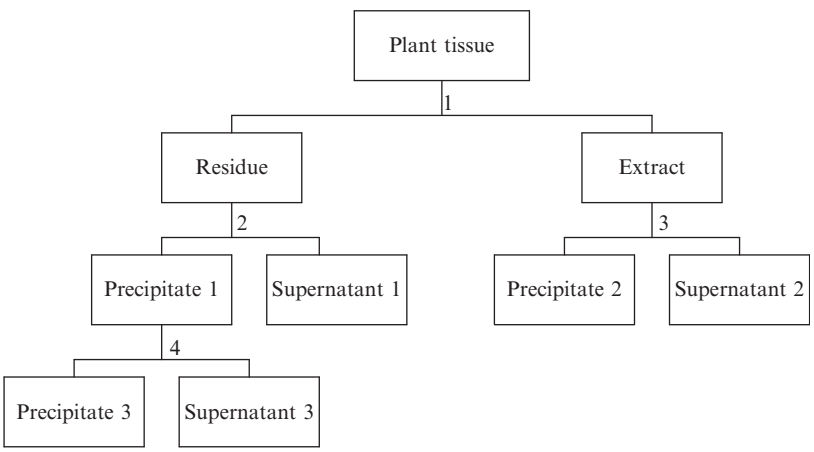
In the earlier Kursanov method, phytic acid and $P_i$ are removed from the TCA extract by precipitation with magnesium chloride and ammonia prior to the addition of barium acetate.[3880]

In the Klein method (Scheme 8-2), which focuses on the acid-insoluble components, the residue from the TCA extraction is separated by fractional precipitation into an ether-soluble fraction (supernatant 1) containing the phospholipids, a magnesium-insoluble fraction (precipitate 2) containing $P_i$, a hot TCA-soluble fraction (supernatant 3) containing the nucleic acids (RNA, DNA), and a hot TCA-insoluble fraction (precipitate 3) containing the phosphoproteins.[3881]

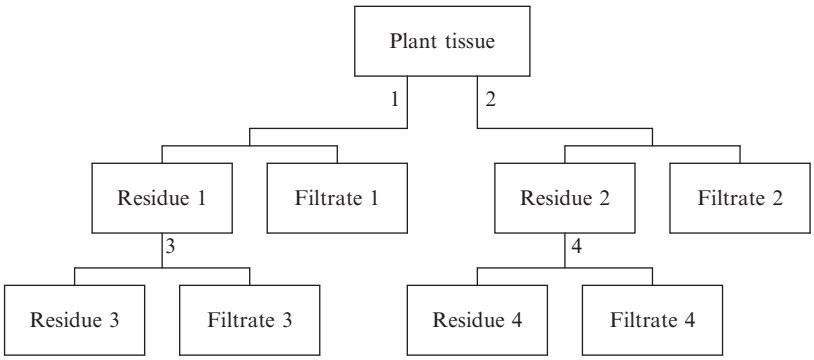
The rest of the entries in Table 8-1 are data from other fractionation schemes that contain one or more precipitation steps.

## Selective Extraction Methods

In the Pons method (Scheme 8-3), the plant tissue is defatted with petroleum ether and then extracted with 0.75*N* trichloroacetic acid (TCA) to remove the acid-soluble compounds (filtrate 3). Another portion of the plant tissue is extracted with benzene-ethanol azeotrope, bp 68.6 °C, to remove the phosphatides (filtrate 2) and then with 2% HCl to remove acid-soluble compounds (filtrate 4). $P_i$ is determined on an aliquot of filtrate 3 by the isobutyl alcohol/molybdate method,[3889] and phytic acid on an aliquot of filtrate 4 by the McCance-Widdowson method.[735] The $P_{sugar}$ content was calculated by subtracting $P_i$ and $P_{phytic\ acid}$




**SCHEME 8-2 Klein Method**. Reagents: (1) 10% TCA. (2) $Et_2O$. (3) $MgCl_2$, $NH_4OH$. (4) 5% TCA (90 °C).




**SCHEME 8-3 Pons Method**. Reagents: (1) Petroleum ether. (2) Benzene-ethanol azeotrope. (3) 0.75*N* TCA. (4) 2% HCl.

from $P_{acid\text{-}soluble}$ and the $P_{nucleic\ acid}$ content by subtracting $P_{acid\text{-}soluble}$ and $P_{phosphatide}$ from $P_{total}$ (Table 8-2).[1034]

In the Martin and Morton method (Scheme 8-4), the plant tissue is defatted with 1:1 chloroform-methanol and then extracted successively with 0.2*N* perchloric acid, 1*N* perchloric acid, and 1*N* sodium hydroxide, giving fractions $P_{acid\ soluble}$ (supernatant 1), $P_{nucl}$ (supernatant 2), and $P_{protein}$ (supernatant 3), respectively.[3892] $P_i$ is determined independently by the Weil-Malherbe and Green method.[204]

Kedrowski[3917] has described an automated procedure for the simultaneous analysis of P and N in $P_{lipid}$, $P_{sugar}$, phytic acid, $P_{nucl}$, and $P_i$ fractions of plant extracts based on the Technicon® autoanalyzer. The method, which has been applied to nearly 1200 tree samples, is estimated to place 90% of the $P_i$ and 85-90% of the $P_{nucl}$ in their proper place in the scheme.

In the Bieleski method (Scheme 8-5), the plant tissue is extracted successively with MCF, formic acid/methanol, and 0.3*M* lithium hydroxide, giving fractions $P_{lipid}$ (supernatant 2), $P_{ester}$ (supernatant 1), and $P_{nucl}$ (supernatant 3), respectively.[327] $P_i$ is determined separately on supernatant 1 by the triethylamine/molybdate method.[3918]

Two other methods for which few details are available are those of Sokolov[3919] and Nilova.[3920]

## Chromatographic Methods

Two-dimensional paper chromatography (PC) and thin-layer chromatography (TLC) have been found to be useful for the separation of individual $P_{lipid}$, $P_{sugar}$, $P_i$, and $P_{nucl}$ compounds from their mixtures in plant extracts (Table 8-3). The solvent systems selected for extraction and separation should be capable of handling all four classes simultaneously, unlike those described in earlier chapters devoted to the individual classes. The following solvent systems are suitable for extraction:

- Methanol/$CHCl_3$/$H_2O$ (12:5:3), then formic acid/ethanol/$H_2O$ (2:5:20)[9]
- Methanol/$CHCl_3$/formic acid/$H_2O$ (12:5:1:2)[327]
- Formic acid (80%), then ethanol (80%)[12]
- Formamide[331]

**Table 8-2** Selective Extraction Methods*

| No. | Plant part | $P_i$ | $P_{lipid}$ | $P_{sugar}$ | $P_{phytate}$ | $P_{nucleotide}$ | $P_{protein}$ | $P_{total}$ | References |
|---|---|---|---|---|---|---|---|---|---|
| | | | | **Pons Method** | | | | | |
| *Arachis hypogaea* L. (Peanut) | | | | | | | | | |
| 1 | Seed, kernel | 7.2 | 9.0 | 11.1 | 70.0 | 2.7 | | 0.334 | 1034 |
| 1 | –, defatted cotyledon | | | | 53.3 | 3.6 | | 0.90 | 847 |
| 1 | –, aleurone grain | | | | 85.6 | 1.6 | | 1.87 | 847 |
| *Cicer arietinum* L. (Bengal Gram) | | | | | | | | | |
| 1 | Seed, mature | 11.2 | 15.7 | | 45.2 | 10.0 | | 0.350 | 3890 |
| 1 | Seed pod, immature and change in seeds and pods from day 20 to day 43[3890] for seed distribution among cotyledon, coat, and embryo, see Lal[3891] | 65.2 | 11.3 | | 9.9 | | | 0.435 | 3890 |
| *Gossypium hirsutum* L. (Cotton) | | | | | | | | | |
| 8 | Seed kernel | 1.8-3.1 | 6.3-7.0 | 7.0-11.0 | 74.5-78.7 | 4.1-5.9 | | 0.965-1.113 | 983 |
| 3 | 6-day seedling, cotyledon | 42.9-54.0 | 11.0-15.2 | 15.2-16.8 | 5.9-8.5 | 8.8-14.5 | | 0.716-1.175 | 984 |
| 3 | –, hypocotyl and root | 59.3-70.2 | 10.5-14.3 | 5.5-12.2 | 0 | 6.9-9.5 | | 0.568-0.753 | 984 |
| Glandless cotton | | | | | | | | | |
| 1 | Seed, defatted kernel | 3.2 | 5.5 | 1.1 | 85.9 | 4.2 | | 1.85 | 985 |
| 1 | –, globoid | 2.5 | 0.5 | | 95.8 | | | 14.21 | 986 |
| *Medicago sativa* L. (Alfalfa) | | | | | | | | | |
| 1 | Seed meal | 44.5 | 16.6 | 21.2 | 2.1 | 15.5 | | 0.283 | 1034 |
| *Oryza sativa* L. (Rice) | | | | | | | | | |
| 8 | White grain | 2.0-3.8 | 0.7-1.1 | 0-13.0 | 34.6-55.0 | 44.0-52.5 | | 0.096-0.121 | 1043 |
| 8 | –, bran | 1.9-2.9 | 0.9-1.2 | 1.3-3.0 | 84.0-93.3 | 1.0-10.4 | | 2.476-2.868 | 1043 |
| 3 | Brown grain | 3.03-3.30 | | | 45.4-62.4 | | | 0.320-0.348 | 1044 |
| 3 | –, bran | 2.15-2.57 | | | 32.9-38.7 | | | 1.955-2.264 | 1044 |
| *Sesamum indicum* L. (Sesame) | | | | | | | | | |
| 1 | Seed | 3.5 | 4.7 | 1.6 | 85.9 | 4.4 | | 0.637 | 1034 |
| *Triticum aestivum* L. (Wheat) | | | | | | | | | |
| 5 | Seed flour | 2.6-3.3 | 3.3-5.4 | 27.0-32.3 | 1.7-6.6 | 55.9-59.0 | | 0.123-0.137 | 16 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Vicia faba* L. (Broad Bean) | | | | | | | | | |
| 1 | Seed, aleurone grain | | | | 64 | 10 | | 1.4 | 812 |
| *Zea mays* L. (Corn) | | | | | | | | | |
| 1 | Seed | 11.4 | 1.4 | 6.4 | 74.4 | 6.4 | | 0.281 | 1034 |
| | | | | **Martin and Morton Method** | | | | | |
| *Beta vulgaris* L. (Silver Beet) | | | | | | | | | |
| 1 | Leaf petiole | | 17.8 | 60.7 | | 10.0 | 8.0 | 0.280 | 3892 |
| 1 | –, mitochondria | 18.7 | 23.8 | 32.8 | | 5.2 | 18.8 | 1.12 | 3892 |
| 1 | –, microsome | 11.5 | 50.9 | 23.6 | | 5.2 | 8.2 | 1.35 | 3892 |
| *Triticum aestivum* L. (Wheat) | | | | | | | | | |
| 1 | Seed, protein body and changes in endosperm, testa-pericarp, and embryo 5-40 daf[3893] | | 2.8 | | 53.9 | 30.9 | 12.4 | 1.78 | 805 |
| *Triticum durum* Desf. (Durum Wheat) | | | | | | | | | |
| 1 | Seed, protein body and changes in endosperm, testa-pericarp, and embryo 5-40 daf[3893] | 4.8 | 51.1 | | 15.6 | 10.5 | 17.0 | 3.52 | 805 |
| *Vicia faba* L. (Broad Bean) | | | | | | | | | |
| 1 | Leaf | | 22.1 | 38.9 | | 34.6 | 4.9 | 1.22 | 3894 |
| 1 | Stem | | 18.5 | 59.0 | | 19.7 | 4.3 | 0.96 | 3894 |
| 1 | Shoot | | 21.9 | 28.3 | | 39.3 | 8.3 | 1.39 | 3894 |
| | | | | **Bieleski Method** | | | | | |
| *Alnus crispa* (Ait.) Pursh. (Green Alder) | | | | | | | | | |
| 1 | Leaf and seasonal changes in leaves and stems | 28.8 | 16.9 | 8.5 negl. | | 28.8 | | 0.059 | 833 |
| *Betula papyrifera* Marsh. (Paper Birch) | | | | | | | | | |
| 1 | Leaf and seasonal changes in leaves and stems | 41.2 | 18.1 | 8.0 negl. | | 26.6 | | 0.199 | 833 |
| *Chionochloa crassiuscula* | | | | | | | | | |
| 1 | Shoot | 66.8 | 7.6 | 12.1 | | 13.4 | | 0.835 | 3895 |
| 1 | Root | 75.4 | 6.4 | 6.0 | | 12.2 | | 1.069 | 3895 |
| *Chionochloa pallens* | | | | | | | | | |
| 1 | Shoot | 52.4 | 12.0 | 13.0 | | 22.5 | | 0.381 | 3895 |
| 1 | Root | 52.0 | 13.4 | 7.1 | | 27.4 | | 0.349 | 3895 |
| *Larix laricina* (Du Roi) K. Koch (American Larch) | | | | | | | | | |
| 1 | Leaf and seasonal changes in leaves and stems | 63.2 | 4.7 | 9.4 negl. | | 13.2 | | 0.106 | 833 |

*$P_{total}$ column: Percent P by weight of plant tissue, fresh weight basis. Other columns: Percent of $P_{total}$.

*Continued*

**Table 8-2** Selective Extraction Methods*—cont'd

| No. | Plant part | $P_i$ | $P_{lipid}$ | $P_{sugar}$ | $P_{phytate}$ | $P_{nucleotide}$ | $P_{protein}$ | $P_{total}$ | References |
|---|---|---|---|---|---|---|---|---|---|
| *Picea mariana* (Mill.) B.S.P. (Black Spruce) | | | | | | | | | |
| 1 | Leaf<br>and seasonal changes in leaves and stems | 31.1 | 21.4 | 6.8 negl. | | 21.4 | | 0.103 | 833 |
| *Solanum tuberosum* L. (Potato) | | | | | | | | | |
| 5 | Tuber | 11.7-31.0 | 5.0-5.9 | 32.5-46.3[a] | 23.4-31.7 | 12.0-15.1 | | 0.205-0.266 | 667 |
| *Spirodela oligorrhiza* (Kurz.) Hegelm. (Duckweed) | | | | | | | | | |
| 1 | Frond tissue culture | 70.7 | 8.2 | 4.7 | 0.14 | 15.5 | | 1.445 | 327 |
| | | | **Other Methods** | | | | | | |
| *Arachis hypogaea* L. (Peanut) | | | | | | | | | |
| 1 | Seed | 4.2 | 4.2 | | 77.9 | 9.8 | | 0.35 | 3896 |
| *Artemisia turanica* H. Krasch. (Wormwood) | | | | | | | | | |
| 1 | Leaf | 17.4 | | 14.7 | 6.5 | 17.9 | | 0.281 | 3897 |
| *Avena sativa* L. (Oats) | | | | | | | | | |
| 1 | Seed<br>and change in root and shoot on germination 2-8 days[875] | 12 | 7 | | 53 | 14 | 6 | 0.55 | 875 |
| *Brassica juncea* L. (Mustard) | | | | | | | | | |
| 1 | Leaf | 32.0 | 27.3 | | | 16.8 | 0.4 | 0.057 | 3898 |
| *Brassica oleracea* L. var. *botrytis* L. (Cauliflower) | | | | | | | | | |
| 2 | Leaf | 20.2-27.3 | 16.8-20.6 | | | 25.6-33.0 | 1.0-1.7 | 0.071-0.158 | 3898 |
| *Cicer arietinum* L. (Chickpea) | | | | | | | | | |
| 1 | Seed | 11.8 | 14.2 | | 24.4 | | 48.9 | 0.436 | 3879 |
| 1 | Seedling (25 days)<br>and data for interval between 0 and 25 days | 82.4 | 8.5 | | 2.7 | | 11.2 | 0.659 | 3879 |
| *Climacoptera crassa* (M.B.) Botsch. | | | | | | | | | |
| 1 | Leaf | 14.5 | | 8.0 | 15.6 | 37.3 | | 0.228 | 3897 |
| *Cucurbita pepo* L. (Vegetable Marrow) | | | | | | | | | |
| 1 | Leaf | 54.0 | 8.6 | | | 19.0 | 0.4 | 0.116 | 3898 |
| *Cuscuta campestris* Yunck. (Field Dodder) | | | | | | | | | |
| 1 | Seed<br>and change during seed development (0-35 daf)[3899] and germination (1-9 days)[3900] | 13.3 | | | 15.9 | 29.6 | | 3.9[b] | 3899 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Glycine max* (L.) Merr. (Soybean) | | | | | | | | |
| 1 | Whole bean | 4.5 | 12.6 | | 74.9 | 5.3 | 0.602 | 3901 |
| 1 | –, protein body | | 9.4 | | 69.2 | 21.6 | 0.43 | 804 |
| 1 | Seed | 3.1 | 9.7 | | 66.9 | 17.2 | 0.54 | 3896 |
| *Gossypium hirsutum* L. (Cotton) | | | | | | | | |
| | Data given for leaf, stem, root, flower, and shoot apex over a 3-month growth period[3902] and for seeds of several spp. during ripening[3903] | | | | | | | |
| *Helianthus annuus* L. (Sunflower) | | | | | | | | |
| 1 | Leaf | 12.7 | 17.5 | | | 48.0 | 3.1 | 0.052 | 3898 |
| 1 | Seed | 2.9 | 2.9 | | 81.9 | 9.2 | | 0.65 | 3896 |
| | and data for seed, leaf, stalk, and calathide during ripening[3904] | | | | | | | |
| *Hordeum vulgare* L. (Barley) | | | | | | | | |
| 1 | Seed | 9.9 | 7.2 | | 63.8 | | 19.1 | 0.379 | 3905 |
| 1 | Grain | 6.9 | 3.2 | 39.5 | 36.8 | 3.0 | 7.1 | | 3906 |
| 1 | Root | 60.5 | | 12.3 | | 8.5 | | | 2586 |
| | and rate of uptake of $P_i$ during first 24 h[2586] | | | | | | | | |
| *Lens culinaris* Medik. (Lentil) | | | | | | | | |
| 1 | Seed | 7.1 | 8.6 | | 62.6 | 14.6 | | 0.40 | 3896 |
| 1 | –, whole flour | 26.2 | 12.1 | | 50.4 | 11.0 | | 0.381 | 3907 |
| *Linum usitatissimum* L. (Flax) | | | | | | | | |
| 1 | Whole plant | 18.6 | 5.4 | 3.7 | 31.2 | 41.1 | | 0.602 | 3908 |
| | and P distribution in stem, leaf, and boll during early growth, flowering, and early yellow ripeness phases | | | | | | | | |
| *Lycopersicon esculentum* Mill. (Tomato) | | | | | | | | |
| 1 | Leaf | 27.9 | 13.8 | | | 26.0 | 1.8 | 0.078 | 3898 |
| *Nicotiana tabacum* L. (Tobacco) | | | | | | | | |
| 1 | Leaf | | | | | | | | 3909 |
| 1 | –, fiber | 9.3 | 35.1 | | | 52.3 | | 0.290 | 3910 |
| 1 | –, chloroplast | | 30.7 | | | 56.8 | | 0.303 | 3910 |
| *Oryza sativa* L. (Rice) | | | | | | | | |
| 1 | Seed | 1.8 | 4.4 | | 77.8 | 9.2 | | 0.29 | 3896 |
| 1 | Seed | tr | 2.2 | | 45.9 | 52.6 | | 0.41 | 3878 |
| 1 | –, embryo | 0.6 | 4.2 | | 82.9 | 12.3 | | 2.70 | 3878 |
| *Phaseolus vulgaris* L. (Bean) | | | | | | | | |
| 1 | Seed | 6.1 | 5.6 | | 73.4 | 12.0 | | 0.50 | 3896 |

*$P_{total}$ column: Percent P by weight of plant tissue, fresh weight basis. Other columns: Percent of $P_{total}$.

*Continued*

**Table 8-2** Selective Extraction Methods*—cont'd

| No. | Plant part | $P_i$ | $P_{lipid}$ | $P_{sugar}$ | $P_{phytate}$ | $P_{nucleotide}$ | $P_{protein}$ | $P_{total}$ | References |
|---|---|---|---|---|---|---|---|---|---|
| *Pisum sativum* L. (Peas) | | | | | | | | | |
| 1 | Seed | 3.9 | 9.2 | | 65.5 | 16.2 | | 0.52 | 3896 |
| 1 | Seed<br>and change during growth 12-40 daf[52] | 6.1 | | 2.8 | 52.0 | 2.0 | | 0.167 | 52 |
| 1 | Cotyledon | 37.3 | | 15.7 | 31.4 | 8.3 | 7.6 | 0.738[c] | 3911 |
| *Ricinus communis* L. (Castor Bean) | | | | | | | | | |
| 1 | Seed | 0.9 | 1.8 | | 85.3 | 8.3 | | 0.76 | 3896 |
| 1 | –, embryo<br>and data for whole embryo, cotyledon, and root-shoot axis over 10 development stages from 10 to 60 dap[3912] | 8 | 4 | | 78 | | | 1.00 | 3912 |
| 1 | –, endosperm<br>and data for whole endosperm and nucellus-integument over 10 developmental stages from 10 to 60 dap[3912] | 3 | 3 | | 93 | | | 0.72 | 3912 |
| *Salsola gemmascens* Pall. | | | | | | | | | |
| 1 | Leaf | 14.5 | | 16.8 | 18.6 | 22.5 | | 0.190 | 3897 |
| *Salsola sclerantha* C.A.M. | | | | | | | | | |
| 1 | Leaf | 31.2 | | 6.3 | 13.8 | 18.4 | | 0.259 | 3897 |
| *Secale cereale* L. (Rye) | | | | | | | | | |
| 1 | Seed | 3.6 | 6.3 | | 77.2 | 7.6 | | 0.39 | 3896 |
| *Solanum tuberosum* L. (Potato) | | | | | | | | | |
| 1 | Leaf | 45.8 | 7.9 | | 22.2 | | 24.3 | 0.428 | 798 |
| *Sorghum bicolor* (L.) Moench (Sorghum) | | | | | | | | | |
| 6 | Seed<br>and change on germination 3-6 days[3913] | 5.0-7.0 | 3.9-4.9 | | 75.7-79.3 | 6.4-8.1 | | 0.387-0.456 | 3913 |
| *Triticum aestivum* L. (Wheat) | | | | | | | | | |
| 1 | Whole plant<br>and data for 18 weeks growth at biweekly intervals | 39.4 | 3.1 | | 57.5 | | | 0.192 | 3914 |
| 3 | Grain | | | | | | | | 3906 |
| 1 | Seed | 3.7 | 5.9 | | 79.0 | 8.5 | | 0.36 | 3896 |
| 1 | Seed | 6.6 | 5.0 | | 68.7 | | 19.7 | 0.309 | 3905 |
| 1 | –, whole germ | 21.3 | 8.8 | | 41.8 | 28.0 | | 1.356 | 3907 |

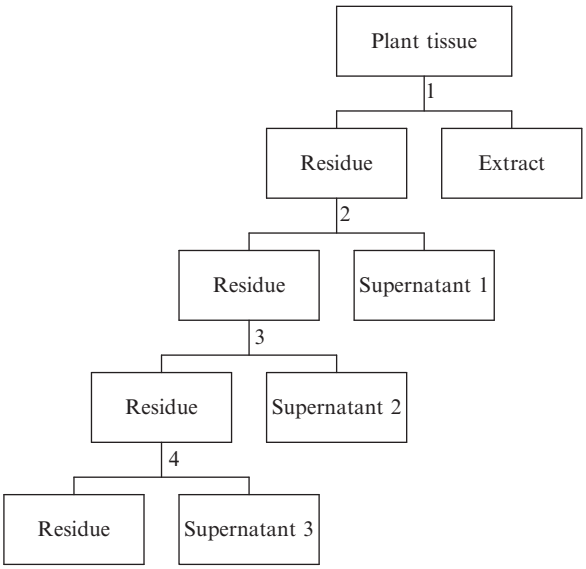
| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Vicia faba* L. (Broad Bean) | | | | | | | | | |
| 1 | Seed | 7.2 | 7.1 | | 65.7 | 12.5 | | 0.46 | 3896 |
| *Vigna radiata* (L.) R. Wilcz. (Mung Bean) | | | | | | | | | |
| 1 | Seed | 4.5 | 7.6 | | 64.4 | | | 0.530 | 3915 |
| *Vigna unguiculata* (L.) Walp. (Cowpea) | | | | | | | | | |
| 1 | Seed | 6.0 | 9.7 | | 30.4 | | | 0.474 | 3915 |
| *Zea mays* L. (Corn) | | | | | | | | | |
| 1 | Seed (yellow) | 3.6 | 10.1 | | 82.6 | | | 0.347 | 3915 |
| 1 | Seed (white) | 4.9 | 15.2 | | 76.5 | | | 0.319 | 3915 |
| 1 | Root | 53.4 | 3.9 | 28.3 | | 16.5 | | 0.032 | 3916 |
| Darso | | | | | | | | | |
| 1 | Seed | 5.1 | 7.3 | | 87.1 | | | 0.312 | 3915 |
| *Zea mays* L. var. *indentata* Sturtev (Dent Corn) | | | | | | | | | |
| 2 | Aerial portion | 36-38 | 12-15 | 29 | | 20-21 | | 0.232-0.270 | 1182 |
| | and change during growth, July 6 to August 22 | | | | | | | | |
| Pasture Grass | | | | | | | | | |
| 1 | Leaf | 80.3 | 1.9 | | 0 | | 17.8 | 0.564 | 3905 |

*$P_{total}$ column: Percent P by weight of plant tissue, fresh weight basis. Other columns: Percent of $P_{total}$.

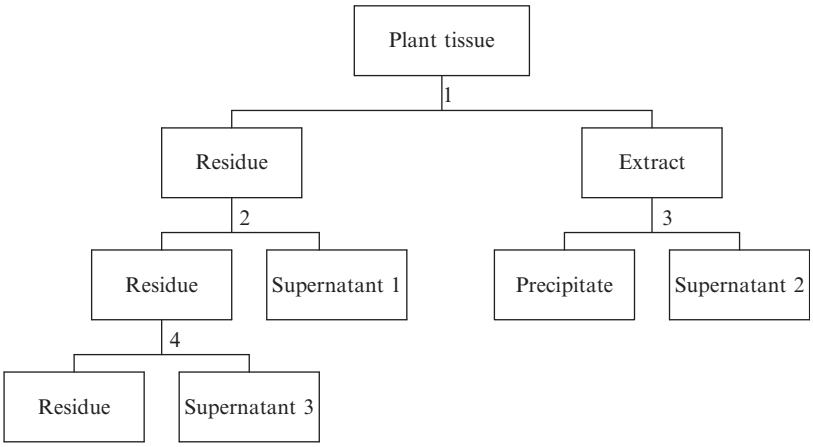
[a]Starch.

[b]µg P/seed.

[c]Mg P/pair of cotyledons.




**SCHEME 8-4 Martin and Morton Method**. Reagents: (1) $CHCl_3$/methanol (1:1). (2) 0.2*N* perchloric acid. (3) 1*N* perchloric acid. (4) 1*N* NaOH.




**SCHEME 8-5 Bieleski Method**. Reagents: (1) Methanol/$CHCl_3$/formic acid/$H_2O$ (MCF, 12:5:1:2). (2) 1% Formic acid in 20% methanol. (3) $CHCl_3$, $H_2O$. (4) 0.3*M* LiOH.

The following pairs of solvent systems are suitable for two-dimensional chromatography:

- *n*-Propanol/$NH_4OH$/$H_2O$ (6:3:1) and *n*-propyl acetate/formic acid/$H_2O$ (11:5:3)[9]
- Isobutyric acid/$NH_4OH$/$H_2O$ (57:4:39) and methanol/1*M* ammonium acetate (7:3)[12]

The method of Wade and Morgan[32] yields good resolution but leaves residual salts on the paper; the method of Wawszkiewicz[29] separates sugar phosphates well but does not separate the nucleotides.[9]

**Table 8-3** Chromatographic Methods*

| No. | Plant part | $P_i$ | $P_{lipid}$ | $P_{sugar}$ | $P_{phytate}$ | $P_{nucleotide}$ | $P_{total}$ | References |
|---|---|---|---|---|---|---|---|---|
| | | | | **PC Method** | | | | |
| *Apium graveolens* L. var. *dulce* (Celery) | | | | | | | | |
| 1 | Petiole, vascular bundle | + | + | + | | + | | 227 |
| *Brassica pekinensis* (Lour.) Rupr. (Pe-tsai) | | | | | | | | |
| 1 | Petiole, vascular bundle | + | + | + | | + | | 227 |
| *Brassica rapa* L. (Turnip) | | | | | | | | |
| 1 | Petiole, vascular bundle | + | + | + | | + | | 240 |
| *Malus sylvestris* (L.) Mill. (Apple) | | | | | | | | |
| 1 | Stem, phloem tissue | + | + | + | | + | | 227 |
| *Nicotiana tabacum* L. (Tobacco) | | | | | | | | |
| 1 | Leaf | + | + | + | | + | | 62 |
| 1 | Leaf | + | | + | | + | | 2627 |
| 1 | Root | + | | + | | + | | 2627 |
| *Persea americana* Mill. (Avocado) | | | | | | | | |
| 1 | Fruit | + | + | + | | + | | 9 |
| *Saccharum officinarum* L. (Sugarcane) | | | | | | | | |
| 2 | Leaf | + | + | + | | + | | 306 |
| 2 | Root | + | + | + | | + | | 306 |
| *Solanum tuberosum* L. (Potato) | | | | | | | | |
| 1 | Tuber | + | + | + | | + | | 9 |
| *Spirodela oligorrhiza* (Kurz.) Hegelm. (Duckweed) | | | | | | | | |
| 1 | Frond tissue culture | + | + | + | | + | | 327 |
| *Triticum aestivum* L. (Wheat) | | | | | | | | |
| 1 | Leaf | + | | + | | + | | 331 |
| *Zea mays* L. (Corn) | | | | | | | | |
| 1 | Root | + | | + | | + | | 12 |
| | | | | **PC/PE Method** | | | | |
| *Triticum aestivum* L. (Wheat) | | | | | | | | |
| 1 | Leaf | + | | + | | + | | 331 |
| | | | | **TLC Method** | | | | |
| *Brassica pekinensis* (Lour.) Rupr. (Pe-tsai) | | | | | | | | |
| 1 | Petiole, vascular bundle | + | + | + | | + | | 36 |
| *Bryophyllum tubiflorum* Harv. (Chandelier Plant) | | | | | | | | |
| 1 | Phylloides | + | + | + | | + | | 3346 |
| *Cuscuta reflexa* Roxb. (Dodder) | | | | | | | | |
| 1 | Callus culture | + | + | + | | + | | 33 |
| *Helodea densa* | | | | | | | | |
| 1 | Callus culture | + | + | + | | + | | 33 |
| *Isoetes duriei* | | | | | | | | |
| 1 | Callus culture | + | + | + | | + | | 33 |
| *Lemna gibba* L. (Gibbous Duckweed) | | | | | | | | |
| 1 | Callus culture | + | + | + | | + | | 33 |
| *Ophioglossum lusitanicum* | | | | | | | | |
| 1 | Callus culture | + | + | + | | + | | 33 |

*$P_{total}$ column: Percent P by weight of plant tissue, fresh weight basis. Other columns: Percent of $P_{total}$.

*Continued*

**Table 8-3** Chromatographic Methods*—cont'd

| No. | Plant part | $P_i$ | $P_{lipid}$ | $P_{sugar}$ | $P_{phytate}$ | $P_{nucleotide}$ | $P_{total}$ | References |
|---|---|---|---|---|---|---|---|---|
| *Ophioglossum vulgatum* | | | | | | | | |
| 1 | Callus culture | + | + | + | | + | | 33 |
| *Salix triandra* L. | | | | | | | | |
| 1 | Phloem exudate | + | + | + | | + | | 309 |
| *Selaginella denticulata* | | | | | | | | |
| 1 | Callus culture | + | + | + | | + | | 33 |
| *Sinapis alba* L. (White Mustard) | | | | | | | | |
| 1 | Callus culture | + | + | + | | + | | 33 |
| *Tillandsia usneoides* | | | | | | | | |
| 1 | Callus culture | + | + | + | | + | | 33 |
| *Vicia faba* L. (Broad Bean) | | | | | | | | |
| 1 | Callus culture | + | + | + | | + | | 33 |
| *Yucca flaccida* H.A.W. | | | | | | | | |
| 1 | Phloem exudate | + | + | + | | + | | 309 |
| *Zea mays* L. (Corn) | | | | | | | | |
| 1 | Root | + | | + | | + | | 12 |
| | **TLC/TLE Method** | | | | | | | |
| *Brassica pekinensis* (Lour.) Rupr. (Pe-tsai) | | | | | | | | |
| 1 | Petiole, vascular bundle | + | + | + | | + | | 36 |
| | **Cellulose Column Method** | | | | | | | |
| *Fragaria* spp. (Strawberry) | | | | | | | | |
| 1 | Leaf | 78.4 | | 21.2[a] | | | 0.025 | 8 |
| *Pisum sativum* L. (Peas) | | | | | | | | |
| 1 | Seed | 13.4 | | 5.9[a] | 80.7 | | 0.187 | 8 |
| *Solanum tuberosum* L. (Potato) | | | | | | | | |
| 1 | Tuber | 85.3 | | 5.3[a] | 18.8 | | 0.032 | 8 |
| | **IEC Method** | | | | | | | |
| *Agropyron desertorum* (Fisch.) Schult. (Crested Wheatgrass) | | | | | | | | |
| 1 | Seed and change on germination 6-48 h | + | + | + | | + | | 831 |
| *Citrus sinensis* (L.) Osbeck (Orange) | | | | | | | | |
| 1 | Juice | + | + | + | | + | | 248 |
| *Lycopersicon esculentum* Mill. (Cherry Tomato) | | | | | | | | |
| 1 | Seed | + | + | + | | + | | 24 |
| *Phaseolus vulgaris* L. (Kidney Bean) | | | | | | | | |
| 1 | leaf | + | | + | | + | | 22 |
| *Pisum sativum* L. (Snap Peas) | | | | | | | | |
| 1 | Seed | + | + | + | | + | | 24 |
| *Spinacia oleracea* L. (Spinach) | | | | | | | | |
| 1 | Leaf chloroplast | + | + | + | | + | | 20 |
| | **HPLC Method** | | | | | | | |
| *Glycine max* (L.) Merr. (Soybean) | | | | | | | | |
| 1 | Leaf | | | + | | + | | 26 |
| *Poa annua* L. (Annual Bluegrass) | | | | | | | | |
| 1 | Root | + | | | + | + | | 696 |
| *Solanum tuberosum* L. (Potato) | | | | | | | | |
| 1 | tuber | + | | | + | + | | 696 |

*$P_{total}$ column: Percent P by weight of plant tissue, fresh weight basis. Other columns: Percent of $P_{total}$.

[a]Including $P_{nucleotide}$.

A few two-dimensional separations have been performed in which paper electrophoresis (PE) or thin-layer electrophoresis (TLE) was substituted for PC or TLC in either the first or second dimension. The following buffers are suitable for PE or TLE:

- Acetic acid/$NH_4OH$/$H_2O$ (15:1:61:984, pH 3.6)[36]
- Acetic acid/pyridine/$H_2O$ (12.5:7.5:980, pH 4.5)[331]

The preferred coating for the plates used in TLC or TLE is an unbound cellulose powder like Macherey-Nagel MN 300. Silica gel gives inferior results.[36]

Isherwood and Barrett[8] developed a method for separating $P_i$, $P_{phytate}$, and $P_{nucl}$ by two-stage chromatography on a cellulose powder column. Phytic acid, sugars, and amino acids are removed in the first stage by elution with *n*-propanol/$NH_4OH$/$H_2O$ (90.4:0.1:9.5) and $P_i$, $P_{sugar}$, $P_{nucl}$, and organic acids in the second stage by elution with diisopropyl ether/formic acid/*t*-butanol/$H_2O$ (18:6:5:5).

A more useful method is ion exchange chromatography (IEC) on a column containing a strongly basic anion exchange resin such as Dowex 1-X8. Wilson and Harris[831] and Heldt *et al.*[20] used gradient elution with formic acid/ammonium formate, whereas Mori *et al.*[316] and others[22,24,248] used the borate gradient of Khym and Cohn.[21] In some cases, the IEC column was coupled to a Bessman phosphorus autoanalyzer[442] for ease of quantitation.[24,248]

High-performance liquid chromatography (HPLC) is possible on a column containing a strongly basic anion exchange resin,[26,696] but this method is clearly unsuitable for use with crude plant extracts without extensive prior cleanup.

## $^{31}$P Nuclear Magnetic Resonance (NMR) Method

The advent of high field $^{31}$P FT NMR spectroscopy in the early 1980s provided a unique opportunity for study of the behavior of phosphorus compounds in living tissue (Table 8-4). These experiments must be done under aeration to prevent anoxia.[544] The strongest signals are usually those of $P_i$, which shows two signals owing to the difference in pH between the cytoplasmic (pH ~7.1) and vascular (pH ~5.5) environments.[42] G6P, UDPG, ATP, and ADP are readily identifiable in the $^{31}$P NMR spectra of root tips, leaves, and suspension cells. Phytic acid is identifiable in potato tubers and germinated lettuce seeds, but dry seeds show only a broad featureless peak despite their high content of phytic acid and other organic phosphates.[47–49]

In contrast, the $^{31}$P NMR spectra of extracts of plant tissues show much higher resolution, especially when EDTA is added to eliminate the line broadening caused by Mg(II) and other paramagnetic ions. Many more sugar phosphates and nucleotides are identifiable in extracts with perchloric acid[48,50] and other acids,[49] and several phospholipids are identifiable in chloroform-methanol extracts.[1366] These studies are beyond the scope of this chapter and are discussed in detail in other chapters.

**Table 8-4** $^{31}$P NMR Method (*In Vivo*)

| No. | Plant part | Compounds identified | References |
|---|---|---|---|
| *Acer pseudoplatanus* L. (Sycamore Maple) | | | |
| 1 | Cell suspension | $P_i$, G6P, F6P | 46 |
| 1 | Cell suspension | $P_i$, G6P, UDPG, ATP (or UTP), NAD | 51 |
| *Catharanthus roseus* (L.) G. Don (Madagascar Periwinkle) | | | |
| 1 | Cell suspension | $P_i$, G6P | 46 |
| *Glycine max* (L.) Merr. (Soybean) | | | |
| 1 | Cell suspension | $P_i$, G6P | 46 |
| 1 | Seedling cotyledon | $P_i$, $P_{sugar}$ | 47 |
| *Helianthus tuberosus* L. (Jerusalem Artichoke) | | | |
| 1 | Stolon | $P_i$, G6P, ATP, ADP, NAD (or UDPG) | 45 |
| *Lactuca sativa* L. (Lettuce) | | | |
| 1 | Sprout | $P_i$, phytic acid | 48 |
| *Nicotiana tabacum* L. (Tobacco) | | | |
| 1 | Cell suspension | $P_i$, G6P, ATP, ADP | 2629 |
| *Pisum sativum* L. (Peas) | | | |
| 1 | Root tip | $P_i$, G6P, UDPG, NTP, NDP | 526 |
| *Solanum tuberosum* L. (Potato) | | | |
| 1 | Tuber | $P_i$, phytic acid | 43 |
| *Sorghum bicolor* (L.) Moench (Sorghum) | | | |
| 1 | Root tip | $P_i$, G6P, UDPG, ATP (or ADP) | 44 |
| *Spinacia oleracea* L. (Spinach) | | | |
| 1 | Leaf | $P_i$, G6P, UDPG, ATP (or UTP), NAD | 51 |
| *Zea mays* L. (Corn) | | | |
| 1 | Root tip | $P_i$, G6P | 42 |
| 1 | Root tip | $P_i$, G6P, UDPG, ATP (or UTP) | 43 |

## Distribution of Individual Phosphorus Compounds in Plants

The culmination of these efforts was Bieleski's 1968 paper on duckweed (*S. oligorrhiza*), the first to provide a complete balance sheet for phosphorus in a plant tissue.[327] Using PC and TLC methods in combination with $^{32}$P labeling, he was able to identify 98% of the phosphorus compounds in the tissue. *Spirodela*, a minute floating water plant, was ideally suited for this purpose as it grows vegetatively in axenic culture on a completely defined medium, doubling its weight every 2 days. It was grown for several generations in $^{32}P_i$ to provide a uniformly labeled plant tissue. The principal components, in percent of total phosphorus, were $P_i$ (70.7%), RNA (11.1%), PC (3.7%), PE (1.7%), DNA (1.4%), PG (1.1%), and G6P (1.1%). Complete results are given in Tables 8-5. In columns 3 and 4, the data for *S. oligorrhiza* are compared with Bieleski's model $P_{ester}$ pattern for young photosynthetic tissue drawn from a variety of published sources.[1]

**Table 8-5** Distribution of Phosphorus Compounds in *S. oiigorrhiza*

| Phosphorus compound | Spirodela oligorrhiza[a] % of $P_{total}$ | Spirodela oligorrhiza[a] nmol/g | Model tissue[b] nmol/g |
|---|---|---|---|
| Inorganic phosphates | | | |
| $P_i$ | 70.7 | 32,980 | |
| $PP_i$ | 0.170 | 85 | |
| Sugar phosphates | | | |
| G6P | 1.076 | 515 | 200 |
| PGA (s) | 0.522 | 250 | 85 |
| α-GP | 0.405 | 195 | 10 |
| Phosphorylethanolamine | 0.282 | 135 | 20 |
| M6P | 0.263 | 125 | 40 |
| F6P | 0.207 | 100 | 60 |
| SDP? | 0.207 | 100 | |
| G1P | 0.113 | 55 | 15 |
| Phosphorylcholine | 0.113 | 55 | 20 |
| Sucrose P? | 0.094 | 45 | |
| F1,6P | 0.085 | 40 | 20 |
| Gal6P | 0.085 | ~40 | |
| PEP | 0.080 | 38 | 15 |
| 6-PG | 0.038 | 19 | 5 |
| TP | 0.033 | 15 | 12[c] |
| Pentose P | 0.019 | 10 | 13 |
| Phosphorylserine | | | 5 |
| Se7P | | | 2 |
| Inositol phosphates | | | |
| Phytic acid | 0.139 | 70 | 15-300 |
| $InsP_2$? | 0.113 | 55 | |
| $InsP_3$ | 0.078 | 40 | |
| Phospholipids | | | |
| PC | 3.67 | 1735 | 630 |
| PE | 1.74 | 820 | 350 |
| PG | 1.08 | 510 | 300 |
| PI | 0.55 | 260 | 130 |
| PS | 0.16 | 75 | 50 |
| PA | 0.06 | 35 | 20 |
| DPG | | | 20 |
| Nucleotides | | | |
| ATP | 0.638 | 300 | 100 |
| UDPG | 0.357 | 170 | 80 |
| ADP | 0.275 | 130 | 30 |
| UTP | 0.264 | 130 | 40 |
| UMP | 0.227 | 110 | 5-40 |
| UDP | 0.175 | 85 | 50 |
| GTP | 0.086 | 42 | 10 |
| UDPX | 0.085 | 40 | |
| GDP | 0.045 | 22 | 5 |
| NAD? | 0.042 | 20 | 45 |

*Continued*

**Table 8-5** Distribution of Phosphorus Compounds in *S. oiigorrhiza*—cont'd

| Phosphorus compound | Spirodela oligorrhiza[a] % of $P_{total}$ | Spirodela oligorrhiza[a] nmol/g | Model tissue[b] nmol/g |
|---|---|---|---|
| AMP | 0.030 | 12 | 8 |
| CDP | 0.014 | 7 | 3 |
| Nucl-3′P | 0.014 | 7 | |
| CMP | 0.005 | 2 | 1 |
| GMP | 0.005 | 2 | 1 |
| CTP | | | 10 |
| ADPG | | | 25 |
| GDPG | | | 2 |
| NADP | | | 7 |
| Nucleic acids | | | |
| RNA | 11.10 | 5230 | |
| DNA | 1.442 | 680 | |
| RNA-P? | 0.186 | 90 | |
| RNA-$P_2$? | 0.124 | 60 | |

[a]Bieleski.[327]
[b]Bieleski.[1]
[c]DHAP.

# Appendices

## Appendix A: Changes Occurring During Germination

All references to studies that are concerned primarily with changes that occur during germination are gathered together in this appendix, regardless of the nature of the phosphorus compound. No data are given and no attempt has been made to avoid duplication. For further details see the cited references:

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| *Acer platanoides* L. (Norway Maple) | | | |
| 1 | Seed (axis, cotyledon) | PC, PE, PG, PI | 3921 |
| *Actinidia deliciosa* Liang and Ferg. (Kiwi) | | | |
| 1 | Seed | ATP | 2452 |
| *Agropyron desertorum* (Link.) Schult. (Crested Wheatgrass) | | | |
| 1 | Seed | $P_{hexose}$, phytic acid, $InsP_2$, $InsP_3$, $InsP_4$, $InsP_5$, ADP, ATP, UTP, UDPX, $P_i$ | 831 |
| *Allium porrum* L. (Leek) | | | |
| 1 | Seed | ATP, GTP, CTP, UTP, UDPG | 2458 |
| *Amaranthus caudatus* L. (Love-Lies-Bleeding) | | | |
| 1 | Seed | Phytic acid | 3922 |
| *Amaranthus cruentus* L. (Purple Amaranth) | | | |
| 1 | Seed | Phytic acid | 3922 |
| *Amaranthus* spp. | | | |
| 2 | Seed | Phytic acid | 3923 |
| *Amaryllis vittata* Ait. (Amaryllis) | | | |
| 1 | Pollen | G3P, DHAP, PEP, F1,6P | 226 |
| 1 | Pollen | AMP, ADP, ATP | 2461 |
| *Arachis hypogaea* L. (Peanut) | | | |
| 6 | Seed | Phytic acid | 846 |
| 1 | Seed | PC, PE, PG, PA, DPG | 1483 |
| 1 | Seed | ATP | 2462,2463 |
| 1 | Seed (axis, cotyledon) | ATP | 3924 |

*Continued*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| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| 1 | Seed (cotyledon, embryonic axis) | Total soluble nucleotides | 3925 |
| –, ssp. *fastigiata* (Spanish Peanut) | | | |
| 1 | Seed ( embryonic axis) | AMP, ADP, ATP | 2465 |
| –, ssp. *hypogaea* Virginia (Peanut) | | | |
| 1 | Seed (embryonic axis) | AMP, ADP, ATP | 2465 |
| *Avena nuda* L. Naked (Oats) | | | |
| 1 | Seed | Phytic acid | 3923 |
| *Avena sativa* L. (Oats) | | | |
| 2 | Seed | Phytic acid | 861 |
| 1 | Seed | Phytic acid | 748,3923,3926 |
| 1 | Seed (embryo) | PGA, G1P, F6P, HDP, phytic acid | 14 |
| 1 | Seed | 3-PGA, PEP, G6P, F2,6P, ATP | 232 |
| 1 | Seed | NAPE | 1497 |
| 1 | Seed | NAD(P) | 3927 |
| 1 | Seed (leaf, root, endosperm) | FMN, FAD | 3600 |
| 1 | Seed | TDP | 3787 |
| 1 | Seed (shoot, root, endosperm) | $P_i$, $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_{protein}$ | 875 |
| *Avena strigosa* Schreb. (Bristle Oats) | | | |
| 1 | Seed | Phytic acid | 861 |
| *Avena strigosa* × *Avena brevis* | | | |
| 1 | Seed | Phytic acid | 861 |
| *Bauhinia purpurea* L. (Purple Bauhinia) | | | |
| 1 | Seed (cotyledon, root, hypocotyl) | PEP | 234 |
| *Benincasa hispida* (Thunb.) Cogn. (Wax Gourd) | | | |
| 1 | Seed | PC, PE, PI, PS | 1512 |
| *Beta vulgaris* L.(Sugar Beet) | | | |
| 1 | Seed | AMP, ADP, ATP | 2763 |
| 2 | Seed | ATP, UDPG | 3928 |
| 2 | Seed | UDPG, UDPGal | 481 |
| *Betula palyrifera* Marsh (White Birch) | | | |
| 1 | Seed | ATP | 3929 |
| *Brassica campestris* L. (Turnip Rape) | | | |
| 2 | Seed | Phytic acid | 886 |
| 1 | Seed | ATP | 2490 |
| *Brassica chinensis* L. (Pak-Choi) | | | |
| 1 | Seed | ATP | 2491 |

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| *Brassica juncea* L. Czern. (Indian Mustard) | | | |
| 1 | Seed | Phytic acid, $P_i$ | 3930 |
| *Brassica napus* L. (Rape) | | | |
| 2 | Seed | Phytic acid | 3931 |
| 1 | Seed | Phytic acid | 3932 |
| 4 | Seed (Canola) | Phytic acid | 886 |
| 1 | Seed (embryo) | PC, PE, PG, PA, LPC, LPA | 3933,3934 |
| 1 | Seed (hull) | PC, PE | 3935 |
| 2 | Seed (pod) | AMP, ADP, ATP | 3936 |
| –, ssp. *oleifera* (Winter Rape) | | | |
| 2 | Seed | AMP, ADP, ATP | 2477 |
| *Brassica oleracea* L. ssp. *botrytis* L. (Cauliflower) | | | |
| 1 | Seed | AMP, ADP, ATP | 2477 |
| *Brassica pekinensis* (Lour.) Rupr. (Chinese Cabbage) | | | |
| 1 | Seed | ATP | 2491 |
| *Cajanus cajan* (L.) Huth (Pigeon Pea) | | | |
| 1 | Seed | Phytic acid | 3937 |
| 6 | Seed | Phytic acid | 898 |
| *Camellia sinensis* L. (Tea) | | | |
| 1 | Pollen | PC, PE, PI | 1558 |
| *Canavalia ensiformis* (L.) DC (Jackbean) | | | |
| 1 | Seed | Phytic acid | 3938 |
| *Cannabis sativa* L. (Hemp) | | | |
| 1 | Seed | Phytic acid | 3939 |
| *Carthamus tinctorius* L. (Safflower) | | | |
| 1 | Seed | PC, PE, PG, PI | 3940 |
| 1 | Seed (cotyledon) | PC, PE, PG, PI, PA | 1570 |
| 1 | Seed | ATP | 2491 |
| *Carum copticum* (L.) Benth. and Hook. (Bishop's Weed) | | | |
| 1 | Seed (cotyledon, root) | PC, PE, PI, LPE | 3941 |
| *Cassia absus* L. (Pig's Senna) | | | |
| 1 | Seed | PC, PE, LPC, LPE | 1575 |
| *Cassia fistula* L. (Golden Shower) | | | |
| 1 | Seed | PC, PE, LPC, LPE | 1575 |
| *Cassia occidentalis* L. (Coffee Senna) | | | |
| 1 | Seed | PC, PE, LPC, LPE | 1575 |
| *Chenopodium quinoa* Willd. (Quinoa) | | | |
| 2 | Seed | Phytic acid, $InsP_3$, $InsP_4$, $InsP_5$ | 916 |
| *Chenopodium rubrum* L. (Red Goosefoot) | | | |
| 1 | Seed | AMP, ADP, ATP, NAD, NADH, NADP, NADPH | 2508 |

*Continued*

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| *Cicer arietinum* L. (Chickpea, Bengal Gram) | | | |
| 1 | Seed | G3P, DHAP, PEP, G6P, F6P, F1,6P, AMP, ADP, ATP | 247 |
| 2 | Seed | Phytic acid | 3942 |
| 1 | Seed | Phytic acid | 924,925,1065, 3879,3890, 3943,3944 |
| 1 | Seed | PC | 927,3879 |
| 1 | Seed | PC, PE | 3945 |
| 1 | Seed | cAMP | 2786 |
| 1 | Seed (pod) | $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$ , $P_i$, $P_{total}$ | 3890 |
| 1 | Seed (cotyledon, embryo, coat) | $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_{protein}$, $P_i$, $P_{totao}$ | 3891 |
| 1 | Seed | $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_{protein}$, $P_i$, $P_{total}$ | 3879 |
| *Cichorium intybus* L. (Chicory) | | | |
| 1 | Seed | Phytic acid | 2767 |
| *Citrullus vulgaris* Schrad. (Watermelon) | | | |
| 1 | Seed (cotyledon) | F2,6P | 492 |
| 1 | Seed (cotyledon, root) | PC, PE, PI, LPE | 1589 |
| *Cocos nucifera* L. (Coconut) | | | |
| 1 | Seed (endosperm) | cAMP | 2789 |
| *Corchorus capsularis* L. (Jute) | | | |
| 1 | Seed | AMP, ADP, ATP | 2521 |
| *Coriandrum sativum* L. (Coriander) | | | |
| 2 | Seed | Phytic acid | 3946 |
| 1 | Seed (endosperm) | PC | 1611 |
| *Corylus avellana* L. (European Hazel) | | | |
| 1 | Seed | PC, PE, PG, PI, PA, NAPE | 1612 |
| 1 | Seed (kernel) | PC, PE, PI | 1613 |
| 1 | Seed | AMP, ADP, ATP, UMP | 2522 |
| *Crotolaria juncea*. L. (Sunn Hemp) | | | |
| 1 | Pollen | PC, PE, PG, PI, PS, PA | 1620 |
| *Cucumis sativus* L. (Cucumber) | | | |
| 1 | Seed | Phytic acid | 941 |
| 1 | Seed (cotyledon) | AMP, ADP, ATP | 2524 |
| 1 | Seed | NAD, NADH | 3442 |
| *Cucurbita moschata* Duch. (Warty Squash) | | | |
| 1 | Seed (leaf thylakoid membrane) | PG | 1632 |
| *Cuphea lanceolata* Ait. (Cigar Flower) | | | |
| 1 | Seed (embryo) | PC | 3947 |

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| *Cuscuta campestris* Yunck (Field Dodder) | | | |
| 1 | Seed | $P_{phytate}$, $P_{DNA}$, $P_{RNA}$, $P_i$, $P_{total}$ | 3899,3900 |
| *Cyclobalanopsis globosa* Lin and Liu | | | |
| 1 | Seed | AMP, ADP | 2534 |
| *Echinochloa cruz-galli* ssp. *praticola* (Barnyard Grass) | | | |
| 1 | Seed | ATP | 2544 |
| *Echinochloa oryzicola* Yasing. Rice (Barnyard Grass) | | | |
| 1 | Seed | NADP(H) | 3444 |
| *Elaeis guineensis* Jacq (Oil Palm) | | | |
| 1 | Seed (kernel) | PC | 3948 |
| *Eleusine coracana* (L.) Gaertn. (Ragi) | | | |
| 15 | Seed | Phytic acid | 960 |
| *Foeniculum vulgare* Mill. Fennel | | | |
| 1 | Seed | Phytic acid | 964 |
| *Glycine max* (L.) Merr. (Soybean) | | | |
| 1 | Seed | Phytic acid | 1329,3930, 3949–3952 |
| 1 | Seed (embryonic axis) | Phytic acid | 974 |
| 1 | Seed | PC, PE, PG, PI, PS, PA, DPG, NAPE | 3953 |
| 1 | Seed | PC, PE, PG, PI, PA, DPG | 1801 |
| 1 | Seed | PC, PE, PI, PS, PA, DPG, phytoglycolipid | 3954 |
| 4 | Seed | PC, PE, PG, PI, PA, DPG, NAPE | 3955 |
| 1 | Seed (cotyledon) | PC, PE, PG, PI, PA, DPG | 3956,3957 |
| 1 | Seed (cotyledon, axis) | PC, PE, PG, PI, LPE | 3958 |
| 1 | Seed | PC, PE molecular species | 2093 |
| 1 | Seed | NAPE | 1497 |
| 1 | Seed | AMP, ADP, ATP, NAD, NADH, NADP, NADPH | 2554 |
| 1 | Seed | AMP, ADP, ATP, GMP, GDP, GTP, CMP, CTP, UMP, UDP, UTP, NAD | 2552 |
| 1 | Seed (cotyledon) | AMP, ADP, ATP, GMP, GTP, UDP, UDPG, NADP | 2553 |
| 1 | Seed | TMP, TDP, TTP | 3780 |
| 1 | Seed | TDP | 3789 |
| *Gossypium barbadense* L. (Sea Island Cotton) | | | |
| 1 | Seed | PC, PE, PI, PS, LPC | 1705 |
| 1 | Seed (kernel) | PC, PE, PI, PS, LPC | 1707 |
| *Gossypium hirsutum* L. (Upland Cotton) | | | |
| 1 | Seed | α-GP, 3-PGA, G1P, F6P, F1,6P | 3959 |
| 1 | Seed | 3-PGA, F6P, F1,6P, phytic acid | 3960 |
| 1 | Seed | Phytic acid | 984 |

*Continued*

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| 1 | Seed (aleurone grain) | Phytic acid | 3961 |
| 1 | Seed | PC, PE, PI, PA | 3962 |
| 1 | Seed | PC, PE, PG, PI, PA, DPG | 3963 |
| 1 | Seed | PC, PI | 3964 |
| 1 | Seed | ATP | 2491 |
| 1 | Seed | AMP, ADP, ATP, GMP, GTP, UMP, UDP, UTP, TTP | 3965 |
| 2 | Seed | AMP, ADP, ATP, GMP, GDP, GTP, CMP, CDP, CTP, UMP, UDP, UTP | 2572 |
| 1 | Seed | TDP | 3789 |
| 1 | Seed | $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_i$, $P_{total}$ | 3903 |
| *Gossypium* spp. (Cotton) | | | |
| 1 | Seed | PC | 3966 |
| *Helianthus annuus* L. (Sunflower) | | | |
| 1 | Seed | Phytic acid | 810,3939 |
| 1 | Seed | Phytic acid, $InsP_3$, $InsP_4$ | 3967 |
| 1 | Seed | PC, PE, PG, PI, PS, PA | 3968 |
| 1 | Seed (cotyledon, oil bodies) | PC, PE, PI, PS | 3969 |
| 1 | Seed | PA | 3970 |
| 1 | Seed | $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_{protein}$, $P_{\alpha\text{-}GP}$, $P_i$, $P_{total}$ | 3904 |
| *Hibiscus cannabinus* L. (Kenaf) | | | |
| 1 | Seed | PC, PE, PG, PI, PA, NAPE, NALPE | 1738 |
| *Hordeum distichon* Alef. (Two-Rowed Barley) | | | |
| 1 | Seed | LPC (starch-bound) | 3971 |
| –, ssp. *nutans* (Rode) Alef. | | | |
| 1 | Seed | G3P, DHAP, G1P, G6P, F6P, F1,6P, ADP, ATP | 267 |
| *Hordeum hexastichon* Alef. ssp. *parallelum* Kŏrn (Six-Rowed Barley) | | | |
| 1 | Seed | AMP, ADP, ATP, GMP, GTP, CMP, UMP, UTP | 2581 |
| *Hordeum vulgare* L. (Barley) | | | |
| 2 | Seed | G1P, G6P, F6P, UDPG | 502 |
| 1 | Seed (starch) | LPC, LPE, LPI | 3972 |
| 1 | Seed | Phytic acid | 993,3926 |
| 1 | Seed | Phytic acid, no lower InsPs | 3973 |
| 1 | Seed (embryo) | AMP, ADP, ATP, UMP, UDP | 3357 |
| 1 | Seed (endosperm) | Total soluble nucleotides | 3974 |
| 1 | Seed | cAMP | 2800 |
| 1 | Seed | cGMP | 2801 |
| 1 | Seed | TDP | 3791 |

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| 1 | Seed (embryo, endosperm) | $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_{protein}$, $P_{RNA}$, $P_{DNA}$, $P_i$, $P_{total}$ | 996,3885,3906 |
| *Iva imbricata* Walter (Seacoast Marsh Elder) | | | |
| 1 | Seed | TDP | 3789 |
| *Kalanchoë blossfeldiana* v. Poelln. (Flaming Katy) | | | |
| 1 | Seed | AMP, ADP, ATP | 2595 |
| *Lablab purpureus* (L.) (Sweet Hyacinth Bean) | | | |
| 1 | Seed | Phytic acid | 3942 |
| *Lactuca sativa* L. (Lettuce) | | | |
| 1 | Seed | PEP, AMP, ADP, ATP | 276 |
| 1 | Seed | Phytic acid | 1005,3975 |
| 1 | Seed | Phytic acid, InsPs | 48 |
| 1 | Seed | AMP, ADP, ATP | 3976 |
| *Lens culinaris* Medik. (Lentil) | | | |
| 2 | Seed | Phytic acid | 1008 |
| 1 | Seed | Phytic acid | 1065,3937 |
| *Lilium henryi* Bak. (Lily) | | | |
| 1 | Pollen | AMP, ADP, ATP | 2606 |
| *Lilium longiflorum* Thunb. (Trumpet Lily) | | | |
| 1 | Pollen | Phytic acid | 1012 |
| 1 | Pollen | PC, PE, PG, PI, PA, PIP | 2360 |
| 1 | Pollen | PC, PE | 1769 |
| *Limnanthes alba* Hart. ex Benth. (Meadowfoam) | | | |
| 1 | Seed (cotyledon) | PC, PE, PA | 1770 |
| *Linum usitatissimum* L. (Flax) | | | |
| 1 | Seed | Phytic acid | 941,3886 |
| 1 | Seed | PC, PE, PI, PS, LPC, LPE | 1771 |
| 1 | Seed (cotyledon) | PC, PE, PG, PI, PA | 1570 |
| *Lupinus albus* L. (White Lupine) | | | |
| 1 | Seed | Phytic acid, no lower InsPs | 1020 |
| *Lupinus angustifolius* L. (Blue Lupine) | | | |
| 1 | Seed | Phytic acid | 1021 |
| *Lupinus luteus* L. (Yellow Lupine) | | | |
| 1 | Seed | Phytic acid, $InsP_3$, $InsP_4$, $InsP_5$ | 1020 |
| 1 | Seed | Phytic acid, $InsP_4$, $InsP_5$ | 1333 |
| 1 | Seed (axis, cotyleon) | ATP | 2610 |
| *Lycopersicon esculentum* Mill. (Tomato) | | | |
| 1 | Seed | Phytic acid | 1027 |
| 1 | Seed | NAD, NADH | 3442 |
| *Machilus thunbergii* Sieb. and Zucc. | | | |
| 1 | Seed | AMP, ADP, ATP | 2619 |
| 1 | Seed | AMP, ADP | 2534 |

*Continued*

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| *Macrotyloma uniflorum* (Lam.) Verdc. (Horse Gram) | | | |
| 1 | Seed | Phytic acid | 1029 |
| *Medicago sativa* L. (Alfalfa) | | | |
| 1 | Seed | PC, PE, PG, PI, DPG | 3977,3978 |
| 1 | Seed | PLP, PMP | 3872 |
| *Michelia compressa* (Maxim.) Sargent | | | |
| 1 | Seed | AMP, ADP | 2534 |
| *Neolitsea parvigemma* (Hayata) Kanak. and Sas. | | | |
| 1 | Seed | AMP, ADP | 2534 |
| *Nicotiana sylvestris* Speg. and Comes | | | |
| 1 | Pollen | PC, PE, PG, PI, PA, DPG | 1818 |
| *Nicotiana tabacum* L. (Tobacco) | | | |
| 1 | Seed | PC, PE, PG, PI, PA | 3979,3980 |
| 1 | Seed | TDP | 3789 |
| *Oenothera biennis* L. (Evening Primrose) | | | |
| 1 | Seed | PC, PE, PG, PI | 1826 |
| *Olea europaea* L. (Olive) | | | |
| 1 | Pollen | PC, PE, PI, PA | 1829 |
| *Oryza sativa* L. (Rice) | | | |
| 1 | Seed | F2,6P | 514 |
| 1 | Seed, dehulled | F2,6P | 3981 |
| 1 | Seed | Phytic acid | 694,783,1187, 1218,2632,3982 |
| 1 | Seed (aleurone particle) | Phytic acid | 1048,1185 |
| 1 | Seed | PC, LPC | 3983 |
| 1 | Seed (coleoptile) | PC, PE, PG, PI, PS, PA, DPG | 1840 |
| 1 | Seed | ATP | 2491,2632 |
| 1 | Seed (embryonic axis) | AMP, ADP, ATP | 2634 |
| 1 | Seed (embryo, endosperm, bran) | ATP | 3984 |
| 1 | Seed (kernel, hull) | ATP | 3985 |
| 1 | Seed | NAD, NADH, NADP, NADPH | 3456 |
| 3 | Seed | $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_{RNA}$, $P_{DNA}$, $P_i$, $P_{total}$ | 3986 |
| 1 | Seed (embryo, pericarp, endosperm) | $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_{protein}$, $P_i$, $P_{total}$ | 3882 |
| 1 | Seed | $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_i$, $P_{total}$ | 1052 |
| *Papaver dubium* L. (Field Poppy) | | | |
| 1 | Pollen | PC, PE, PG, PI, PS, PA, DPG | 3987 |
| *Papaver somniferum* L. (Opium Poppy) | | | |
| 1 | Seed | Phytic acid | 810 |

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| *Pennisetum glaucum* (L.) R. Br. (Pearl Millet) | | | |
| 1 | Seed | Phytic acid | 3988 |
| *Perilla frutescens* (L.) Britt. (Perilla Mint) | | | |
| 1 | Seed | Phytic acid | 3952 |
| –, ssp. *japonica* (Egoma) | | | |
| 2 | Seed | PC, PE, PG, PI, PS, LPC | 1862 |
| *Petroselinum crispum* (Mill.) A. W. Hill (Parsley) | | | |
| 1 | Seed | $P_1$, $P_{lipid}$, $P_{nucleotide}$, $P_i$ | 792 |
| *Petunia hybrida* L. (Petunia) | | | |
| 1 | Pollen | Phytic acid | 3989 |
| 1 | Pollen | PC, PE, PI, PA (no PG, PS, PIP or $PIP_2$) | 2363 |
| *Phacelia tanacetifolia* Benth. (Fiddleneck) | | | |
| 1 | Seed | NAD(P)(H) | 2644 |
| 1 | Seed | Phytic acid | 1065 |
| *Phaseolus coccineus* L. (Scarlet Runner Bean) | | | |
| 1 | Seed | F2,6P | 518 |
| 1 | Seed | Phytic acid | 1065 |
| *Phaseolus lunatus* L. (Lima Bean) | | | |
| 1 | Seed | PC, PE, PG, PI | 3990 |
| *Phaseolus vulgaris* L. (Bean) | | | |
| 1 | Seed | F6P, F2,6P, ATP | 521 |
| 1 | Seed (cotyledon) | Phytic acid | 3991,3992 |
| 2 | Seed | Phytic acid | 3993,3994 |
| 1 | Seed (radicle, plumule) | PC | 3966 |
| 1 | Seed | AMP, ADP, ATP | 3995 |
| 1 | Seed | NAD(P) | 3996 |
| 1 | Seed | FMN,FAD | 3997 |
| 1 | Seed (cotyledon, hypocotyl, root) | Free and total thiamine | 3998 |
| 1 | Seed | TDP, vitamin $B_1$ | 3999 |
| *Phellodendron wilsonii* Hayata and Kaneh. (Cork Tree) | | | |
| 1 | Seed | AMP, ADP | 3929 |
| *Picea abies* (L.) Karst. (Norway Spruce) | | | |
| 1 | Seed (embryo, endosperm) | G6P, ADP, ATP | 523 |
| *Picea pungens* Engelm. (Colorado Spruce) | | | |
| 1 | Pollen | Phytic acid | 818 |
| *Pinus banksiana* Lamb. Jack Pine | | | |
| 1 | Seed | ATP | 3929 |
| *Pinus densiflora* Sieb. and Zucc. (Japanese Red Pine) | | | |
| 1 | Pollen | cAMP, cGMP | 2827 |

*Continued*

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| *Pinus mugo* Turra (Mugo Pine) | | | |
| 1 | Pollen | ATP, GTP, CTP, UTP, UDPGlc, UDPGal | 2669 |
| *Pinus pinea* L. Italian (Stone Pine) | | | |
| 1 | Seed | PLP | 3866 |
| *Pinus ponderosa* Laws. (Ponderosa Pine) | | | |
| 1 | Seed (embryo, endosperm) | AMP, ADP, ATP | 2670 |
| 1 | Pollen | Phytic acid | 818 |
| *Pinus sylvestris* L. (Scotch Pine) | | | |
| 1 | Seed (embryo, endosperm) | G6P, ADP, ATP | 523 |
| 1 | Pollen | NAD(P), NAD(P)H | 3465 |
| *Pisum sativum* L. (Peas) | | | |
| 1 | Seed (cotyledon) | G6P, F6P | 2679 |
| 2 | Seed (embryo) | F2,6P | 295 |
| 3 | Seed | Phytic acid | 1083 |
| 1 | Seed | Phytic acid | 1084,3911, 3937,4000 |
| 1 | Seed | Phytic acid, $InsP_3$, $InsP_4$, $InsP_5$, | 1333 |
| 1 | Seed | PC | 4001 |
| 1 | Seed | PC, PE | 4002 |
| 1 | Seed | PC, PE, PG, PI | 3990 |
| 1 | Seed | PC, PE, PA, LPC | 4003 |
| 1 | Seed | PC, PE, PI, PS, DPG, LPC, LPE | 4004 |
| 1 | Seed | NAPE | 1497 |
| 1 | Seed | ATP | 2682 |
| 1 | Seed | AMP, ADP, ATP | 2846 |
| 1 | Seed (cotyledon) | AMP, ADP, ATP, GMP, UMP, IMP, NAD, NADH, NADP, NADPH | 2679,3471 |
| 1 | Seed | UDPG | 4005 |
| 1 | Seed | UDPFru | 3359 |
| 1 | Seed | NAD | 3466 |
| 1 | Seed | NAD, FAD | 4006 |
| 1 | Seed | TMP, TDP, TTP | 3780 |
| 1 | Seed | TDP | 3789,3795 |
| 1 | Seed (coleoptile, leaf, root) | PLP | 3873 |
| *Podocarpus macrophyllus* (Thunb.) Sweet (Yew Plum Pine) | | | |
| 1 | Seed | AMP, ADP | 2534 |
| *Prunus dulcis* (Mill.) D. A. Webb (Cherry) | | | |
| 1 | Seed (kernel) | PC, PE, PG, DPG | 4007 |

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| *Prunus persica* (L.) Batsch (Peach) | | | |
| 1 | Seed (endocarp) | PC, PE, PI, PS | 3086 |
| *Pseudotsuga menziesii* (Mirb.) Franco (Douglas Fir) | | | |
| 1 | Seed | Total soluble nucleotides | 4008 |
| *Psophocarpus tetragonolobus* (L.) DC (Winged Bean) | | | |
| 1 | Seed | Phytic acid | 1101 |
| 1 | Seed | PC, PE, PG, PI, PS, DPG | 1927 |
| *Raphanus sativus* L. (Radish) | | | |
| 1 | Seed | ATP | 2491 |
| 1 | Seed | AMP, ADP, ATP | 2691 |
| *Ricinus communis* L. (Castor Bean) | | | |
| 1 | Seed | 3-PGA, PEP, G6P, F6P, F1,6P | 302 |
| 1 | Seed (endosperm) | F2,6P | 528 |
| 1 | Seed | Phytic acid | 1106 |
| 1 | Seed | Phytic acid (no lower InsPs) | 684 |
| 1 | Seed (cotyledon) | Phytic acid | 813 |
| 1 | Seed (endosperm) | Phytic acid | 1105,4009 |
| 1 | Seed (aleurone grain) | Phytic acid | 4009 |
| 1 | Seed (endosperm) | PC, PE, PG, PS, PA, DPG | 4010 |
| 1 | Seed | NAD, NADP, NMN | 3476 |
| 1 | Seed (embryo, cotyledon, endosperm) | $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_i$, $P_{total}$ | 3912 |
| *Secale cereale* L. (Rye) | | | |
| 2 | Seed | Phytic acid | 3926 |
| 4 | Seed | Phytic acid | 1110 |
| 1 | Seed | Phytic acid | 3923,4011 |
| 1 | Seed (chromatin) | PC, PE, PI | 1959 |
| 1 | Seed (nuclear matrix) | PC, PE, PI | 1960 |
| 1 | Seed | AMP, ADP, ATP | 2699 |
| 1 | Seed (leaf, root, endosperm) | FMN, FAD | 3600 |
| 1 | Seed (embryo, endosperm) | $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_{protein}$, $P_{RNA}$, $P_{DNA}$, $P_i$, $P_{total}$ | 996 |
| *Sesamum indicum* L. (Sesame) | | | |
| 1 | Seed | Phytic acid | 3952 |
| *Sinapis alba* L. (White Mustard) | | | |
| 1 | Seed | PC, PI, PA | 4012 |
| 1 | Seed | AMP, ADP, ATP | 2702 |
| *Solanum tuberosum* L. (Potato) | | | |
| 1 | Seed (core) | PC, PE | 4013 |
| *Sophora japonica* L. (Japanese Pagoda Tree) | | | |
| 1 | Seed | PC, PE, PI, PS, PA, NAPE, LPC, NALPE | 1987 |

*Continued*

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| *Sorghum bicolor* (L.) Moench. (Sorghum) | | | |
| 1 | Seed | Phytic acid | 4014 |
| 4 | Seed | Phytic acid | 4015 |
| 2 | Seed | UMP, UDPG, ADPG | 3369 |
| 6 | Seed | $P_i$, $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$ | 3913 |
| *Striga asiatica* (L.) Kuntze (Witchweed) | | | |
| 1 | Seed | PC, PE, PG, PI | 2003 |
| *Trifolium incarnatum* L. (Crimson Clover) | | | |
| 1 | Seed | AMP, ADP, ATP | 4016 |
| *Trifolium repens* L. (White Clover) | | | |
| 1 | Seed | Phytic acid | 1128 |
| *Trifolium subterraneum* L. (Sub Clover) | | | |
| 1 | Seed | Phytic acid | 693 |
| *Trigonella foenumgraecum* L. (Fenugreek) | | | |
| 1 | Seed | Phytic acid | 1131,4017,4018 |
| 1 | Seed | PC, PE, PG, PI, PS, PA, LPC | 4019 |
| 1 | Seed | AMP, ADP, ATP, UMP | 2716 |
| *Triticum aestivum* L. (Wheat) | | | |
| 1 | Seed (root, shoot) | G3P, DHAP, F1,6P | 330 |
| 1 | Seed (endosperm) | G3P, DHAP, G1P, G6P, F6P, F1,6P, F2,6P | 537 |
| 1 | Seed (endosperm) | G1P, G6P, G1,6P, F6P, F1,6P, F2,6P | 538 |
| 1 | Grain | HMP, HDP, phytic acid | 3887 |
| 3 | Seed | Phytic acid | 3926 |
| 1 | Seed | Phytic acid | 693,925,1137, 3923,3930, 4020–4022 |
| 1 | Seed (bran) | Phytic acid | 4023 |
| 2 | Seed (aleurone particle) | Phytic acid | 1185,4024 |
| 1 | Seed (testa, embryo, aleurone, endosperm) | Phytic acid, ATP, $P_i$ | 789 |
| 2 | Seed | Phytic acid, InsP, $InsP_2$, $InsP_3$, $InsP_4$, $InsP_5$ | 1226 |
| 1 | Seed | Phytic acid, $InsP_4$ | 3967 |
| 1 | Seed | No lower InsPs | 1198 |
| 1 | Grain (embryo removed) | PC | 4025 |
| 1 | Seed | PC, PE, PI, PS, PA, NAPE, LPC, LPE, LPA, NALPE | 2026 |
| 1 | Seed (endosperm) | PC, PE, PG, PI, PS, PA, DPG, NAPE, LPC. LPE, LPA, NALPE | 4026 |
| 2 | Seed | PC, PE, PG, PI, PS, LPC | 4027 |

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| 1 | Seed (kernel) | PC, PE | 4028 |
| 1 | Seed (coleoptile, mitochondria) | PC, PE, PS, PA, DPG, LPE | 4029 |
| 1 | Seed (chromatin) | PC, PE, PI, PS, DPG, LPC | 2029 |
| 1 | Seed | ATP | 2491,2695 |
| 1 | Seed | AMP, ADP, ATP, GDP, GTP, CTP, UDP, UTP | 2725 |
| 1 | Seed | AMP, ADP, ATP | 2720,2722 |
| 1 | Seed (embryo) | AMP, ADP, ATP | 4030,4031 |
| 1 | Seed (embryo) | ATP, GTP, CTP, UTP | 2734 |
| 1 | Seed (endosperm, testa, pericarp) | AMP, ADP, ATP, ADPG, UMP, UDP, UTP, UDPG, NAD | 2723 |
| 2 | Seed | UDPG | 3372 |
| 2 | Grain | AMP, ADP, ATP, NAD, NADH, DADP, NADPH | 4032 |
| 1 | Seed | NAD, NADH, NADP, NADPH | 3416,3456 |
| 1 | Seed (embryo) | NAD, NADH, NADP, NADPH | 3486 |
| 1 | Seed | Total soluble nucleotides | 4033 |
| 2 | Seed (embryo, endosperm) | Total soluble nucleotides | 2768 |
| 1 | Seed | TDP | 3798,4034 |
| 1 | Seed (leaf, root) | PLP | 3873 |
| 4 | Seed | $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_{protein}$, $P_{RNA}$, $P_{DNA}$, $P_i$, $P_{total}$ | 996,3906 |
| 1 | Seed | $P_{sugar}$, $P_{phytate}$, $P_i$, $P_{total}$ | 4035 |
| 1 | Seed (embryo, endosperm) | $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_{protein}$, $P_{RNA}$, $P_{DNA}$, $P_i$, $P_{total}$ | 3885 |
| 1 | Grain (testa/pericarp, embryo, endosperm) | $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_{protein}$, $P_{RNA}$, $P_{DNA}$, $P_i$, $P_{total}$ | 3893 |
| *T. aestivum* × *Secale cereale* (× *Triticosecale* Wittm.) Triticale | | | |
| 5 | Seed | Phytic acid | 1146,4036 |
| 4 | Seed | ATP | 2717 |
| *Triticum durum* Desf. (Durum Wheat) | | | |
| 1 | Seed | Phytic acid | 4037 |
| 2 | Seed (embryo) | AMP, ADP, ATP | 2737 |
| 1 | Grain (testa/pericarp, embryo, endosperm) | $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_{protein}$, $P_{RNA}$, $P_{DNA}$, $P_i$, $P_{total}$ | 3893 |
| *Triticum spelta* L. (Spelt) | | | |
| 1 | Seed | PC | 4038 |
| *Uniola paniculata* Walter (Sea Oats) | | | |
| 1 | Seed | TDP | 3789 |

*Continued*

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| *Vicia faba* L. (Faba Bean) | | | |
| 2 | Seed | Phytic acid | 4039,4040 |
| 1 | Seed | Phytic acid | 810,1065 |
| 8 | Seed | Phytic acid | 4041 |
| 1 | Seed | PC, PE, PG, PI | 3990 |
| 1 | Seed | NAPE | 1497 |
| 1 | Seed | AMP, ADP, ATP, GMP, GTP, CMP, UMP, CTP, UTP | 4042 |
| 1 | Seed | AMP, ADP, ATP, GMP, GTP, CMP, UMP, UTP, UDPX, NAD | 2738 |
| 1 | Seed | TDP | 4043 |
| –, ssp. *minor* L. (Small Horse Bean) | | | |
| 1 | Seed | Phytic acid, $InsP_3$, $InsP_4$, $InsP_5$ | 1333 |
| *Vigna aconitifolia* (Jacq.) Mar. (Moth Bean) | | | |
| 1 | Seed | Phytic acid | 1029,1158 |
| *Vigna angularis* (Willd.) Ohwi and Ohashi (Adzuki Bean) | | | |
| 1 | Seed | Phytic acid | 3951 |
| 1 | Seed | PC, PE, PI | 4044 |
| *Vigna mungo* (L.) Hepper (Black Gram) | | | |
| 1 | Seed (cotyledon, axis) | G6P, 6-PG, F6P, ATP | 540 |
| 1 | Seed | Phytic acid | 3942,3993,4045 |
| 6 | Seed | Phytic acid | 898 |
| 1 | Seed | PC, PE, PG, PI, PS, PA, DPG, NAPE, LPC, LPE, NALPE | 1384 |
| *Vigna mungo* × *Vigna radiata* | | | |
| 1 | Seed | Phytic acid | 1165 |
| *Vigna radiata* (L.) Wilcz. (Mung Bean, Green Gram) | | | |
| 1 | Seed | G3P | 4046 |
| 1 | Seed | Phytic acid | 925,1051,3943, 3951,3952, 4047,4048 |
| 5 | Seed | Phytic acid | 4049 |
| 1 | Seed | Phytic acid, lower InsPs | 693 |
| 1 | Seed | Phytic acid, $InsP_1$, $InsP_2$, $InsP_3$, $InsP_4$, $InsP_5$, | 4050 |
| 1 | Seed | PC, PE, PG, PI, PS, PA | 2053 |
| 1 | Seed | PC, PE, PI, PA | 2059 |
| 1 | Seed | AMP, ADP, ATP | 2524 |
| 1 | Seed (hypocotyl) | AMP, CMP | 4051 |
| 1 | Seed | AMP, ADP, ATP, GMP, GDP, GTP, CMP, UMP | 4016 |
| 1 | Seed | AMP, ADP, ATP, UDP, UDPGlc, UDPGlcNAc | 4052 |

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| 1 | Seed | AMP, ADP, ATP, CMP, UMP, UTP, UDPX, X=Glc, Gal, Xyl, Ara, Rha, GlcNAc; GDPMan, NADP | 2744 |
| 1 | Seed | AMP, ADP, ATP, GMP, GDP, GTP, CMP, CDP, CTP, UMP, UDP, UTP, UDPX, X=Glc, Gal, Ara, Xyl, GlcA, GalA, GalNAc; GDPMan | 2742 |
| 1 | Seed (plumule, radicle, cotyledon) | FMN, FAD | 3585 |
| 1 | Seed | TDP | 3789 |
| *Vigna sesquipedalis* (L.) Fruh. Yard-Long Bean | | | |
| 1 | Seed (cotyledon, hypocotyl, root) | NAD, NADH, NADP, NADPH | 3411 |
| *Vigna umbellata* (Thunb.) Ohwi and Ohashi (Rice Bean) | | | |
| 5 | Seed | Phytic acid | 4049 |
| *Vigna unguiculata* (L.) Walp. (Cowpea) | | | |
| 1 | Seed | Phytic acid | 824,1069, 3993,4053 |
| 1 | Seed (plumule, radicle, cotyledon) | FMN, FAD | 3585 |
| *Xanthium pennsylvanicum* Wallr. (Cocklebur) | | | |
| 1 | Seed (cotyledon, axis) | AMP, ADP, ATP | 4054 |
| *Zea mays* L. (Corn) | | | |
| 3 | Grain | Phytic acid | 4055 |
| 1 | Seed | Phytic acid | 1180,1182 |
| 1 | Seed | PC | 3966 |
| 1 | Seed | PC, PE, PA, LPC | 4003 |
| 1 | Seed (kernel) | PC, PE, PG, PI, PA, DPG, LPC | 4056 |
| 1 | Seed | PC, PG, PI | 4057 |
| 1 | Seed (germ, endosperm, pericarp) | PC, PE, PI, PA, LPC, LPE | 4058 |
| 1 | Seed | AMP, ADP, ATP, GMP, GDP, GTP, CMP, CTP, UMP, UDP, UTP, NAD, NADP | 3497 |
| 1 | Seed | ATP | 4059 |
| 2 | Seed (embryo) | ATP | 2760 |
| 1 | Seed (embryo) | ATP | 4060 |
| 1 | Seed (embryo, endosperm) | AMP, ADP, ATP | 2753 |
| 1 | Seed | cAMP | 4061 |
| 2 | Grain | NAD, NADP, NAAD, NMN | 3494 |
| 1 | Seed | NAD, NADH, NADP, NADPH | 3408 |
| 1 | Seed (root, shoot) | NAD, NADH, NADP, NADPH | 3498 |

*Continued*

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| 1 | Seed (axis, scutellum, endosperm) | Total soluble nucleotides | 4062 |
| 1 | Seed | TMP, TDP, TTP | 3780 |
| 1 | Seed | TDP | 3789,4034,4063 |
| 1 | Seed | $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_i$, $P_{total}$ | 791 |

# Appendix B: Changes Occurring During Growth and Senescence

All references to studies that are concerned primarily with changes that occur during growth and senescence are gathered together in this appendix, regardless of the nature of the phosphorus compound. No data are given and no attempt has been made to avoid duplication. For further details see the cited references:

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| *Acanthus mollis* L. (Boar's Breech) | | | |
| 1 | Leaf | NAD(P) | 4064 |
| *Acer pseudoplatanus* L. (Sycamore maple) | | | |
| 1 | Cell culture | PC, PE, PI, PA, LPC, LPE, NALPE | 4065 |
| 1 | Cell culture | AMP, ADP, ATP, NAD, NADH, NADP, NADPH | 2449 |
| *Actinidia deliciosa* Liang and Ferg. (Kiwi) | | | |
| 1 | Callus culture | G6P | 475 |
| *Ailanthus glandulosa* Desf. (Chinese Sumac) | | | |
| 1 | Cataphylls | PC, PE, PG, PI, PS, PA, DPG | 4066 |
| *Albizia lebbeck* (L.) Benth. (Lebbek Tree) | | | |
| 1 | Leaf | PEP | 223 |
| *Alnus crispa* (Ait.) Pursh. (Green Alder) | | | |
| 1 | Leaf, bud, terminal stem | $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_i$, $P_{total}$ | 833 |
| *Arabidopsis thaliana* (L.) Heynh (Mouse-Ear Cress) | | | |
| 1 | Leaf | PC, PE, PG, PI | 4067 |
| *Arachis hypogaea* L. (Peanut) | | | |
| 1 | Leaf | PEP | 228 |
| *Artemisia turanica* H. Krasch. (Wormwood) | | | |
| 1 | Leaf | 3-PGA, phytic acid, $P_{nucleotide}$, $P_i$ | 3897 |
| *Arum maculatum* L. (Cuckoopint) | | | |
| 1 | Spadix | 2-PGA, 3-PGA, PEP, G1P, G6P, F6P, F1,6P | 230 |
| 1 | –, mitochondria | PC, PE, PG, PI, PS, PA, DPG | 1490 |

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| *Avena sativa* L. (Oats) | | | |
| 1 | Leaf | FMN, FAD | 3601 |
| *Bauhinia purpurea* L. (Purple Bauhinia) | | | |
| 1 | Fruit | PEP | 233 |
| *Bauhinia variegata* L. (Orchid Tree) | | | |
| 1 | Flower bud | PEP | 235 |
| 1 | Leaf, flower | PEP | 233 |
| *Beta vulgaris* L. (Sugar Beet) | | | |
| 1 | Root | PC, PE, PG, PI, PS, PA, DPG | 1515 |
| 1 | Root | AMP, ADP, ATP, GMP, GDP, CMP, UMP | 2485 |
| 1 | Leaf, root | ADP, ATP | 4068 |
| *Betula papyrifera* Marsh. (Paper Birch) | | | |
| 1 | Leaf, bud, terminal stem | $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_i$, $P_{total}$ | 833 |
| *Betula pendula* Roth (European White Birch) | | | |
| 1 | Leaf | F2,6P, ADP, ATP | 4069 |
| 1 | Leaf, bud | PC, PE, PG, PI, PS | 4070 |
| *Brassica campestris* L. (Turnip Rape) | | | |
| 1 | Pod, deseeded | G3P, DHAP, 3-PGA, RuBP, F6P, F1,6P, F2,6P | 238 |
| 1 | Flower | PC, PE, PG, PI, DPG | 4071 |
| *Brassica napus* L. ssp. *oleifera* (Winter Rape) | | | |
| 2 | Stem, apex | PC | 4072 |
| 2 | Leaf, shoot apex | ATP | 2493 |
| *Brassica oleracea* L. ssp. *capitata* L. (Cabbage) | | | |
| 6 | Leaf | AMP, ADP, ATP | 4073 |
| *Cajanus cajan* (L.) Huth (Pigeon Pea) | | | |
| 1 | Leaf | PEP | 4074 |
| 1 | Flower | PEP | 241 |
| *Canavalia ensiformis* (L.) DC (Jack Bean) | | | |
| 1 | Root nodule | PC, PE, PG, PI, PS | 1559 |
| *Cannabis sativa* L. (Hemp) | | | |
| 1 | Leaf | AMP, ADP, ATP | 2501 |
| *Capsicum annuum* L. (Sweet Pepper) | | | |
| 1 | Fruit, pericarp | F2,6P | 4075 |
| 1 | Fruit (chloroplast, chromoplast, microsomal membrane) | PC, PE, PG, PI, PA | 1564 |
| *Catharanthus roseus* (L.) G. Don (Madagascar Periwinkle) | | | |
| 1 | Cell suspension culture | G3P, DHAP, 2-PGA, 3-PGA, PEP, G1P, G6P, F6P, F1,6P | 4076 |
| 1 | Cell suspension culture | UDPX, X=Glc, Gal, Xyl, Ara, GlcA | 3347 |
| *Centaurea moschata* L. (Sweet Sultan) | | | |
| 1 | Leaf | PEP | 244 |

*Continued*

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| *Chenopodium rubrum* L. (Red Goosefoot) | | | |
| 1 | Cell suspension culture | UDPG | 2509 |
| 1 | Stem | PC, PE, PG, PI, PA, DPG | 4077 |
| *Cicer arietinum* L. (Chickpea, Bengal Gram) | | | |
| 1 | Root | PC, PE, PG, PS, PA, DPG | 4078 |
| *Cichorium intybus* L. (Chicory) | | | |
| 1 | Explant leaf | AMP, GMP, CMP, UMP | 2511 |
| 1 | Root | NAD, NADH, NADP, NADPH | 3433 |
| *Citrus hassaku* hort. ex Tanaka (Hassaku) | | | |
| 1 | Fruit juice | PC, PE | 1601 |
| *Citrus junos* (Sieb.) Tanaka (Yuzu) | | | |
| 1 | Leaf | PC, PE, PG | 1598 |
| *Citrus limettioides* Tanaka (Sweet Lemon) | | | |
| 1 | Fruit | AMP, ADP, ATP | 2514 |
| *Citrus limon* L. (Sour Lemon) | | | |
| 1 | Fruit | AMP, ADP, ATP | 2514 |
| 1 | Flower | $P_{acid\text{-}soluble}$, $P_{lipid}$, $P_{protein}$, $P_{RNA}$, $P_{DNA}$ | 4079 |
| 1 | Leaf | $P_{acid\text{-}soluble}$, $P_{lipid}$, $P_{protein}$, $P_{RNA}$, $P_{DNA}$ | 4080 |
| *Citrus medioglobosa* hort. ex Tanaka (Naruto) | | | |
| 1 | Fruit (flavedo) | PC, PE, PI | 4081 |
| *Citrus natsudaidai* Hayata (Sour Orange) | | | |
| 1 | Leaf | PC, PE, PG | 1598 |
| 1 | Fruit juice | PC, PE | 1601 |
| *Citrus sinensis* (L.) Osbeck (Orange) | | | |
| 1 | Leaf | PC, PE, PG, PI, DPG | 1557 |
| 1 | Leaf | ATP | 4082 |
| 1 | Juice vesicles | ADP, ATP, NAD, NADH, NADP, NADPH | 2520 |
| *Citrus tamurana* hort. ex Tanaka (Hyuganatsu) | | | |
| 1 | Fruit juice | PC, PE | 1601 |
| *Climacoptera crassa* (M.B.) Botsch. | | | |
| 1 | Leaf | 3-PGA, phytic acid, $P_{nucleotide}$, $P_i$ | 3897 |
| *Crambe amabilis* But. and Maj. (Crambe) | | | |
| 1 | Various plant parts | PC, PE, PG, PI, PS, PA, NAPE, NALPE, LPC | 1616 |
| *Cucumis sativus* L. (Cucumber) | | | |
| 1 | Leaf | PC, PE, PG, PI | 4083 |
| *Cucurbita pepo* L. (Pumpkin) | | | |
| 1 | Leaf | PC, PE, PG, PI, PS | 1634 |
| 1 | Root | AMP, ADP, ATP, GMP, GDP, CMP, UMP, UDP | 2532 |
| *Datura inoxia* Mill. (Downy Thorn Apple) | | | |
| 1 | Cell suspension culture | AMP, ADP, ATP, GMP, GDP, GTP, CTP, UMP, UDP, UTP, NAD, NADP | 3351 |
| *Daucus carota* L. (Carrot) | | | |
| 1 | Leaf | PC, PE, PG, PI, PS | 1634 |

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| *Diapensia lapponica* L. (Pincushion Plant) | | | |
| 1 | Leafy top | PC, PE, PG | 1653 |
| *Distichlis spicata* (L.) Greene (Coastal Saltgrass) | | | |
| 1 | Leaf | AMP, ADP, ATP | 2542 |
| *Elaeeis guineensis* Jacq. (Oil Palm) | | | |
| 1 | Fruit (mesocarp) | PC, PE, PG, PI, PS, PA, DPG, LPC | 4084 |
| *Erythronium japonicum* Decne (Katakuri) | | | |
| 1 | Leaf | 3-PGA, Ru1,5P | 256 |
| *Evodia rutaecarpa* Hook.f. and Thomson | | | |
| 1 | Fruit | cGMP | 2792 |
| *Fagopyrum esculentum* Moench (Buckwheat) | | | |
| 1 | Leaf | ADP, ATP | 2548 |
| *Fagus sylvatica* L. (European Beech) | | | |
| 1 | Leaf | PC, PE, PG, PI, PS | 1634 |
| *Festuca pratense* Huds. (Meadow Fescue) | | | |
| 2 | Leaf | PC PE, PG, PI, DPG | 1679 |
| *Ficaria verna* Huds. (Lesser Celandene) | | | |
| 1 | Tuber | AMP, ADP, ATP | 2550 |
| *Fraxinus excelsior* L. (European Ash) | | | |
| 1 | Apical and axillary buds | ATP, NTP | 2551 |
| *Glycine max* (L.) Merr. (Soybean) | | | |
| 1 | Leaf | GAP, hexose P | 56 |
| 1 | Leaf | F2,6P | 4085 |
| 1 | Leaf | Phytic acid | 4086 |
| 1 | Root | PC, PE, PG, PI, PA, DPG, NAPE | 1701 |
| *Gossypium arboreum* L. (Tree Cotton) | | | |
| 1 | Fiber | AMP, ADP, ATP | 2567 |
| 1 | Boll (fiber) | NAD, NADP | 2566 |
| *Gossypium barbadense* L. (Sea Island Cotton) | | | |
| 1 | Leaf | 3-PGA, G1P, F1P | 263 |
| 1 | Fiber | AMP, ADP, ATP | 2567 |
| *Gossypium hirsutum* L. (Upland Cotton) | | | |
| 1 | Leaf | TP, 3-PGA, HMP, HDP | 4087 |
| 1 | Boll, fiber | G1P, G6P, UDPX, X = Glc, Gal, Xyl, Ara, Man, Rha, Fuc | 2571 |
| 1 | Whole plant | PC, PE, PI, PA | 4088 |
| 1 | Fiber | PC, PE, PG, PI, PS | 1719 |
| 1 | Leaf (chloroplast) | AMP, ADP, ATP | 4089 |
| 1 | Leaf | $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_i$, $P_{total}$ | 4090 |
| 1 | Leaf, stem, root, flower, shoot apex | $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_i$, $P_{total}$ | 3902 |

Continued

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| *Helianthus annuus* L. (Sunflower) | | | |
| 1 | Leaf, stalk, calathide | $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_{protein}$, $P_{\alpha\text{-GP}}$, $P_i$, $P_{total}$ | 3904 |
| 1 | Callus culture | cAMP | 2796 |
| *Helianthus tuberosus* L. (Jerusalem Artichoke) | | | |
| 1 | Tuber (plasmalemma) | PC, PE, PG, PI, PS, PA | 4091 |
| *Hibiscus cannabinus* L. (Kenaf) | | | |
| 1 | Leaf, bud, stem, flower, root | PC, PE, PG, PI, PA, NAPE, NALPE | 1738 |
| *Hibiscus rosa-sinensis* L. (Hibiscus) | | | |
| 1 | Leaf | PC, PG | 1566 |
| *Hordeum vulgare* L. (Barley) | | | |
| 1 | Leaf | G6P, F2,6P | 3358 |
| 2 | Leaf | PC, PE, PG, PI, PA; no PS | 4092 |
| 2 | Leaf segments | PC, PE, PG, PI | 4093 |
| 1 | Leaf (chloroplast) | PC, PG | 4094 |
| 1 | Leaf | AMP, ADP, ATP, NAD, NADP | 4095 |
| 1 | Leaf | FMN, FAD | 3601 |
| 2 | Seedling | UDPG | 502 |
| *Impatiens balsamina* L. (Garden Balsam) | | | |
| 1 | Leaf | PC, PE, PG, PI, PS | 1634 |
| *Ipomoea aquatica* Forssk. (Swamp Morning Glory) | | | |
| 1 | Cell suspension culture | PC, PE, PG | 4096 |
| *Ipomoea batatas* (L.) Lam. (Sweet Potato) | | | |
| 1 | Root | AMP, ADP, ATP, UMP, UTP, UDPG, ADPG | 2592 |
| *Larix laricina* (Du Roi) K. Koch. (American Larch) | | | |
| 1 | Leaf, bud, terminal stem | $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_i$, $P_{total}$ | 833 |
| *Larix sibirica* (Siberian Larch) | | | |
| 1 | Cambium | PC, PE, PI, PS, PA, NAPE | 1763,4097 |
| *Lemna gibba* L. (Gibbous Duckweed) | | | |
| 1 | Frond (axenic culture) | Phytic acid | 695 |
| *Lemna paucicostata* Hegelm. (Lesser Duckweed) | | | |
| 1 | Whole plant | cAMP, cGMP | 2805 |
| *Linum usitatissimum* L. (Flax) | | | |
| 1 | Leaf, stalk, boll | $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_i$, $P_{total}$ | 3908 |
| *Lolium multiflorum* Lam. (Italian Ryegrass) | | | |
| 1 | Endosperm cell suspension culture | cAMP | 2807 |
| *Lotus corniculatus* L. (Birdsfoot Trefoil) | | | |
| 1 | Root | Phytic acid | 1016 |
| *Lupinus luteus* L. (Yellow Lupine) | | | |
| 1 | Root nodule | NAD, NADH, NADP, NADPH | 4098 |

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| *Lycopersicon esculentum* Mill. (Tomato) | | | |
| 1 | Fruit | TP, PEP, G6P, F6P, F1,6P | 278 |
| 1 | Fruit | PC, PE, PS, PA, DPG | 1779 |
| 1 | Fruit (pericarp) | PC, PE, PG, PI, PS, PA, DPG | 4099 |
| 1 | Fruit | AMP, ADP, ATP, UMP, UTP, UDPG | 2615 |
| *Malus domestica* Borkh. (Apple) | | | |
| 1 | Fruit | G6P, F6P, 6-PG | 4100 |
| 1 | Stem (cortex) | Phytic acid | 1030 |
| 1 | Shoot (phloem, xylem) | PC, PE, PG, PI | 1791 |
| 1 | Bud (axial, terminal) | PC, PE, PG, PI | 4101 |
| *Mangifera indica* L. (Mango) | | | |
| 1 | Leaf | cAMP | 2787 |
| *Medicago sativa* L. (Alfalfa) | | | |
| 1 | Root | Phytic acid | 1016 |
| *Morus alba* L. (Mulberry) | | | |
| 1 | Shoot | AMP, ADP, ATP | 2624 |
| 1 | Stem, bark | AMP, ADP, ATP | 4102,4103 |
| *Myriophyllum quitense* H.B.K. (Water Milfoil) | | | |
| 1 | Leaf, stem, root | PE, PI | 1810 |
| *Nicotiana suaveolens* Lehm. × *Nicotiana langsdorffii* | | | |
| 1 | Stem | cAMP | 2812 |
| *Nicotiana tabacum* L. (Tobacco) | | | |
| 1 | Leaf | 3-PGA, PEP, G6P | 285 |
| 1 | Leaf | 3-PGA | 4104 |
| 1 | Shoot | 3-PGA, G1P, G6P, F6P, F2,6P | 288 |
| 1 | Root | 3-PGA, G6P, F2,6P | 288 |
| 1 | Cell suspension culture | InsP, $InsP_2$, $InsP_3$ | 1200 |
| 1 | Leaf | PC, PE, PG, PI, PS | 4105 |
| 1 | Leaf, flower (petal, pistil, ovary, anther) | PC, PE, PG, PI, PS, DPG | 1819 |
| 1 | Leaf | AMP, ADP, ATP, GMP, GDP, GTP, CDP, CTP, UMP, UDP, UTP, UDPX (X=Glc, Gal, GlcA, GalA, GlcNAc), GDPG, NAD, NADP | 2628 |
| 1 | Leaf, stem, root, apical bud | cAMP | 2787 |
| 1 | Callus culture | UDPG, ADPG | 3364 |
| 1 | Cell suspension culture | AMP, ADP, ATP, GDP, GTP, CDP, CTP, UMP, UDP, UTP, UDPX (X=Glc, Gal, GalA, GlcNAc), GDPG, NAD, NADP | 4106 |
| 1 | Leaf | FMN, FAD | 3608 |
| 1 | Leaf | $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_{protein}$, $P_i$, $P_{total}$ | 3909 |

Continued

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| *Oryza sativa* L. (Rice) | | | |
| 1 | Seedling | AMP, ADP, ATP, UMP, UDP, UTP, UDPG | 4107 |
| 3 | Leaf | $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_i$, $P_{total}$ | 1052 |
| *Padus racemosa* Lam. (Bird Cherry) | | | |
| 1 | Stem (cortex) | Phytic acid | 1030 |
| *Persea americana* Mill. (Avocado) | | | |
| 1 | Leaf | cAMP | 2787 |
| *Petunia hybrida* hort. (Petunia) | | | |
| 1 | Flower (bud, anther) | Phytic acid | 2363 |
| *Phaseolus vulgaris* L. (Kidney Bean) | | | |
| 1 | Leaf | 2-PGA, G1P, G6P, F6P, F1,6P, AMP, ADP, ATP | 22 |
| 1 | Leaf | PC, PE, PG, PI | 4108 |
| 1 | Leaf | PC, PE, PG, PI, PS | 1634 |
| 1 | Leaf | PC, PG | 1566 |
| 1 | Leaf | PC | 4109 |
| 1 | Leaf (chloroplast envelope membrane) | PC, PG | 4110 |
| 1 | Leaf | AMP, ADP, ATP, GDP, GTP, CTP, UMP, UTP, UDPG, GDPG, NAD, ADPR | 2649 |
| 1 | Leaf | ATP | 2756 |
| 1 | Leaf (petiole, laminae) | AMP, ADP, ATP, GMP, GTP, CMP, CTP, UMP, UTP | 2653 |
| 1 | Root | ATP | 4111 |
| *Picea abies* (L.) Karst. (Norway Spruce) | | | |
| 1 | Needle | G6P, F6P | 4112 |
| 1 | Needle | F6P, F2,6P | 4113 |
| 1 | Needle | $P_1$, G6P, F6P, F2,6P | 530 |
| 1 | Shoot | PC, PE, PI | 2115 |
| *Picea mariana* (Mill.) B.S.P. (Black Spruce) | | | |
| 1 | Leaf, bud, terminal stem | $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_{nucleotide}$, $P_i$, $P_{total}$ | 833 |
| *Pinus nigra* Arnold (Black Pine) | | | |
| 1 | Needle | PC, PE, PG | 1892 |
| *Pinus pinea* L. (Italian Stone Pine) | | | |
| 1 | Leaf | PLP | 3866 |
| *Pinus resinosa* Ait. (Red Pine) | | | |
| 1 | Ovule | ATP | 2671 |
| *Pinus tadea* L. (Loblolly Pine) | | | |
| 1 | Callus culture | cAMP | 2828 |
| *Pisum sativum* L. (Peas) | | | |
| 1 | Development | $P_i$, HMP, HDP, ADP, ATP, GTP, UTP | 52 |
| 1 | Leaf | PC, PA | 4114 |
| 1 | Leaf | PC | 4109 |

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| *Platanus* spp. (Plane Tree) | | | |
| 1 | Leaf | PC, PE, PG, PI, PS | 1634 |
| *Populus gelrica* (Houtz.) Houtz. | | | |
| 1 | Bark | G3P, 3-PGA, E4P, R5P, G1P, G6P, 6-PG, F6P, F1,6P, Se7P | 4115 |
| 1 | Bark (xylem) | AMP, ADP, ATP | 2685 |
| *Populus nigra* L. (Black Poplar) | | | |
| 1 | Bark | G3P, E4P, R5P, G1P, G6P, 6-PG, F6P, F1,6P, Se7P | 298 |
| *Portulaca grandiflora* Hook. (Rose Moss) | | | |
| 1 | Leaf | PEP | 244 |
| *Portulaca oleracea* L. (Purslane) | | | |
| 1 | Leaf | 3-PGA, PEP, $P_{sugar}$ | 4116 |
| *Prunus armeniaca* L. (Apricot) | | | |
| 1 | Flower | $P_{acid\text{-}soluble}$, $P_{lipid}$, $P_{protein}$, $P_{RNA}$, $P_{DNA}$ | 4117 |
| *Prunus avium* (L.) L. (Cherry) | | | |
| 1 | Leaf | PG | 1921 |
| *Prunus mume* Sieb. and Zucc. (Ume Apricot) | | | |
| 1 | Fruit | PC, PE | 4118 |
| *Prunus persica* (L.) Batsch (Peach) | | | |
| 1 | Leaf | $P_{acid\text{-}soluble}$, $P_{lipid}$, $P_{protein}$, $P_{RNA}$, $P_{DNA}$ | 4119 |
| 1 | Flower | $P_{acid\text{-}soluble}$, $P_{lipid}$, $P_{protein}$, $P_{RNA}$, $P_{DNA}$ | 4120 |
| *Pyrus communis* L. (Pear) | | | |
| 1 | Fruit skin | R5P, F1,6P, Se7P | 19 |
| *Raphanus sativus* L. (Radish) | | | |
| 1 | Leaf | PC, PE, PG, PI | 1938 |
| *Ricinus communis* L. (Castor Bean) | | | |
| 1 | Root-shoot axis, nucellus-integument | $P_i$, $P_{sugar}$, $P_{phytate}$, $P_{lipid}$, $P_i$, $P_{total}$ | 3912 |
| *Robinia pseudoacacia* L. (Black Locust) | | | |
| 1 | Bark | PC, PE, PG, PI, PS, DPG | 4121 |
| *Saccharum* hybrid (Sugarcane) | | | |
| 1 | Leaf | 3-PGA, HMP | 4122 |
| *Salsola gemmascens* Pall. | | | |
| 1 | Leaf | 3-PGA, phytic acid, $P_i$, $P_{nucleotide}$ | 3897 |
| *Salsola sclerantha* C.A.M. | | | |
| 1 | Leaf | 3-PGA, phytic acid, $P_i$, $P_{nucleotide}$ | 3897 |
| *Secale cereale* L. (Rye) | | | |
| 1 | Leaf | FMN, FAD | 3601 |
| *Sesamum indicum* L. (Sesame) | | | |
| 1 | Oil bodies, microsomes | PC, PE, PG | 4123 |
| *Solanum acaule* Bitt. (Wild Potato) | | | |
| 1 | Leaf | PC, PE, PG, PI | 1972 |

*Continued*

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| –, ssp. *punae* Juz. | | | |
| 1 | Leaf | PC, PE, PG, PI | 1972 |
| *Solanum acaule* Bitt. ssp. *schreiteri* Buk. | | | |
| 1 | Leaf | PC, PE, PG, PI | 1972 |
| *Solanum demissum* Lindl. (Nightshade) | | | |
| 1 | Leaf | PC, PE, PG, PI | 1972 |
| *Solanum maglia* Schlecht. | | | |
| 1 | Leaf | PC, PE, PG, PI | 1975 |
| *Solanum pamitanae* | | | |
| 1 | Leaf | PC, PE, PG, PI | 1972 |
| *Solanum rybinii* Juz. and Buk. | | | |
| 1 | Leaf | PC, PE, PG, PI | 1972 |
| *Solanum sanctae-rosae* Hawkes | | | |
| 1 | Leaf | PC, PE, PG, PI | 1972 |
| *Solanum tuberosum* L. (Potato) | | | |
| 3 | Tuber | F2,6P, UDPG | 532 |
| 1 | Tuber | TP, 3-PGA, PEP, G1P, G6P, F6P, F1,6P, F2,6P | 533 |
| 2 | Tuber | Starch P, phytic acid | 4124,4125 |
| 6 | Tuber | PC, PE, PI | 4126 |
| 1 | Root, shoot | ADP, ATP | 4127 |
| 1 | Tuber (starch grain) | ADP, ADPG, NAD | 3480 |
| *Sorghum bicolor* (L.) Moench (Sorghum) | | | |
| 1 | Leaf | 3-PGA | 4128 |
| 1 | Leaf (chloroplast) | PC, PG, PI | 2060 |
| *Spartina alterniflora* Loisel. (Smooth Cordgrass) | | | |
| 1 | Leaf | AMP, ADP, ATP | 2542 |
| *Spartina cynosuroides* (L.) Roth | | | |
| 1 | Leaf | AMP, ADP, ATP | 2542 |
| *Spartina patens* (Ait.) Muhl. (Saltmeadow Cordgrass) | | | |
| 1 | Leaf | AMP, ADP, ATP | 2542 |
| *Spinacea oleracea* L. (Spinach) | | | |
| 1 | Leaf | TP, PGA, PEP, G1P, G6P, F6P, F1,6P | 4129 |
| 1 | Leaf | PC, PG | 1566 |
| *Trifolium pratense* L. (Red Clover) | | | |
| 1 | Whole plant | Phytic acid | 1016 |
| *Trifolium repens* L. (White Clover) | | | |
| 1 | Leaf | 6-PG | 474 |
| *Triticum aestivum* L. (Wheat) | | | |
| 1 | Leaf | TP, 3-PGA, RuBP | 4130 |
| 2 | Leaf | PC, PE, PG, PI, PS, PA | 4092 |
| 1 | Leaf | PC, PG | 4131 |
| 1 | Leaf (chloroplast) | PC, PG, PI | 2060 |

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| 1 | Leaf (chloroplast) | PG | 4132 |
| 1 | Stem (apex) | PC | 4072 |
| 1 | Tillering nodes | PC, PE, PG, PI, PS, PA, DPG | 2038 |
| 1 | Stem, leaf, flower | LPC | 4133 |
| 1 | Leaf | AMP, ADP, ATP, NAD, NADP | 4095 |
| 1 | Leaf | AMP, ADP, ATP, UDPG, UDPGlcNAc, NAD, NADP | 3374,4134 |
| 1 | Seedling | UDPG, UDPGal | 537 |
| 1 | Leaf | NAD, NADH, NADP, NADPH | 3460 |
| 1 | Leaf | FMN, FAD | 3601 |
| 1 | Flag leaf | $P_{sugar}$, $P_{lipid}$, $P_i$, $P_{total}$ | 4035 |
| 1 | Leaf, root, tillering node | $P_{sugar}$, $P_{lipid}$, $P_{nucleotide}$, $P_{RNA}$, $P_{DNA}$, $P_i$, $P_{total}$ | 4135 |
| 1 | Whole plant, straw, ears | $P_{phytate}$, $P_{lipid}$, $P_i$, $P_{total}$ | 3914 |
| *Vicia faba* L. (Faba Bean) | | | |
| 1 | Leaf | PG | 2047 |
| 1 | Seedling, pod | AMP, ADP, ATP, GMP, GTP, UMP, UTP, UDPG, NAD | 2738 |
| 1 | Leaf, stem, cotyledon, pericarp, testa and hilum | FMN | 4136 |
| *Vigna mungo* (L.) Hepper (Black Gram) | | | |
| 1 | Root (nodule) | ATP | 2741 |
| *Vigna ratiata* (L.) Wilcz. (Mung Bean) | | | |
| 1 | Leaf (chloroplast) | PC, PG, PI | 2060 |
| *Vigna unguiculata* (L.) Walp. (Cowpea) | | | |
| 1 | Leaf | PC, PE, PG, PI | 4137,4138 |
| *Vinca minor* L. (Periwinkle) | | | |
| 1 | Leaf | PC, PE, PG | 2065 |
| *Vitis vinifera* L. (Wine Grape) | | | |
| 1 | Seedless berry | TP, PEP, G6P, F6P, F1,6P, AMP, ADP, ATP | 333 |
| 1 | Berry | PC, PE, PG, PI, PS, PA, LPC, LPE | 4139 |
| 4 | Vine | FMN, FAD | 3611 |
| *Wolffiella floridana* (Sm.) Thomps. (Water Meal) | | | |
| 1 | Frond (axenic culture) | Phytic acid | 695 |
| *Zea mays* L. (Corn) | | | |
| 1 | Ear | Phytic acid | 810,1181 |
| 1 | Leaf | PC, PG | 1566 |
| 1 | Leaf | PC, PE, PG | 4140 |
| 1 | Leaf (chloroplast) | PC, PG, PI | 2060,4057 |
| 1 | Leaf (chloroplast, thylakoid membrane) | PC, PG, PI, PS | 4141 |
| 1 | Root | PC, PE, PG, PS, PA, DPG | 4078 |
| 1 | Root | PC, PE, PG, DPG | 4142 |
| 1 | Root | ATP | 4143 |

*Continued*

| No. | Plant species | Compounds analyzed | References |
|---|---|---|---|
| 2 | Shoot, apex, leaf | ATP | 2756 |
| 1 | Leaf | AMP, ADP, ATP | 4144 |
| *Zea mays* L. ssp. *indentata* Sturt. (Dent Corn) | | | |
| 2 | Aerial portion | $P_{sugar}$, $P_{lipid}$, $P_{nucleotide}$, $P_i$, $P_{total}$ | 1182 |
| *Ziziphus vulgaris* ssp. *inermis* | | | |
| 1 | Fruit (flesh, stone) | cGMP | 2845 |

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*Amorphophallus campanulatus* (Elephant Yam, Telingo Potato, White Spot Arum), 70*t*, 89*t*
*Amorphophallus konjac* (Konjak), 392*t*
AMP. *See* Adenosine 5′-Phosphate (AMP)
Amur Cork Tree. *See Phyllodendron wilsonii*
*Anacardium occidentale* (Cashew), 89*t*, 223*t*
*Ananas comosus* (Pineapple), 42*t*, 89*t*
*Androsace helvetica* (Swiss Rock Jasmine), 223*t*
*Anethum graveolens* (Dill), 223*t*
*Angelica acutiloba*, 89*t*
*Angelica silvestris* (Woodland Angelica), 413*t*
*Angelica sinensis* (Danggui), 223*t*
Anise. *See Pimpinella anisum*
Anise, Star. *See Illicium verum*
Annatto. *See Bixa orellana*
*Annona cherimola* (Cherimoya), 42*t*
*Annona muricata* (Soursop, Guayabano), 42*t*
*Annona squamosa* (Sweetsop, Ates), 89*t*
*Anomodon viticulosus* (Anomodon Moss), 223*t*
*Anthoceros laevis*, ssp. *Lorbeer*, 223*t*
*Anthriscus cerefolium* (Chervil), 223*t*
*Antirrhinum majus* (Snapdragon), 89*t*, 223*t*
*Apium graveolens* (Celery), 18*t*, 89*t*, 223*t*, 312*t*, 380*t*, 392*t*, 469*t*
  ssp. *dulce*, 223*t*, 312*t*, 392*t*
  ssp. *rapaceum* (Celeriac), 89*t*
*Apodanthera undulata* (Melon-Loco), 223*t*
Apple. *See Malus domestica*
Apricot. *See Prunus armeniaca*
Apricot, Japanese or Ume. *See Prunus mume*
*Aquilegia alpina* (Alpine Columbine), 200*t*
*Aquilegia vulgaris* (European Columbine), 413*t*
*Arabidopsis thaliana* (Mouse-Ear Cress), 42*t*, 178*t*, 189*t*, 200*t*, 223*t*, 312*t*, 490–500
Arabinose 1′-Phosphate (Ara1P), 388*f*
Arabinose 5′-Phosphate (Ara5P), 65
*Arachis hypogaea* (Peanut, Groundnut), 18*t*, 89*t*, 161*t*, 178*t*, 223*t*, 312*t*, 446*t*, 462*t*, 490–500
  ssp. *fastigiata* (Spanish Peanut), 475–490
  ssp. *hypogaea* (Virginia Peanut), 475–490
*Araucaria angustifolia* (Paraná Pine), 89*t*
*Araucaria araucana* (Monkey-Puzzle Tree), 89*t*
*Araucaria bidwillii* (Bunya-Bunya), 89*t*
*Araucaria cunninghamii* (Moreton Bay Pine), 223*t*
*Araucaria heterophylla* (Norfolk Pine), 223*t*
*Arbutus unedo* (Strawberry Tree), 18*t*, 33*t*, 42*t*
*Arctotheca calendula*, 89*t*
*Arenga pinnata* (Sugar Palm), 70*t*, 89*t*
*Aronia melanocarpa* (Chokeberry), 223*t*
Arrowhead. *See Sagittaria sagittifolia*
Arrowhead, Chinese. *See Sagittaria trifolia*
Arrowroot. *See Maranta arundinacea*
Arsenic Bush. *See Senna septentrionalis*

*Artemisia turanica* (Wormwood), 462*t*, 490–500
*Arthrocnemum indicum*, 223*t*
Artichoke, Jerusalem. *See Helianthus tuberosus*
*Artocarpus altilis* (Breadfruit, Rimas), 89*t*
*Artocarpus camansi* (Breadnut), 89*t*
*Artocarpus heterophyllus* (Jackfruit), 89*t*
*Arum maculatum* (Cuckoopint), 18*t*, 42*t*, 70*t*, 223*t*, 392*t*, 490–500
Arum, White Spot. *See Amorphophallus campanulatus*
Ash, European. *See Fraxinus excelsior*
Ash, Japanese. *See Fraxinus mandshurica ssp. japonica*
Ash, Mountain. *See Sorbus commixta*
Ash, White. *See Fraxinus americana*
*Asparagus officinalis* (Asparagus), 312*t*, 455*t*
Aspen, European. *See Populus tremula*
*Asplenium nidus* (Hawaii Birdnest Fern), 413*t*
*Asplenium viride* (Green Spleenwort), 223*t*
Aster. *See Cosmos* spp.
*Astragalus bisulcatus* (Milk Vetch), 89*t*
*Astragalus chinensis* (Chinese Milk Vetch), 223*t*
Aswagandh. *See Withania somnifera*
Ates. *See Annona squamosa*
*Athyrium esculentum* (Vegetable Fern), 89*t*
ATP. *See* Adenosine 5′-Triphosphate (ATP)
*Atrichum angustatum*, 223*t*
*Atrichum haussknechtii*, 223*t*
*Atriplex gmelinic*, 223*t*
*Atriplex patula* (Spreading Orach), 89*t*
*Atriplex prostrata*, 223*t*
*Atropa belladonna* (Belladonna), 223*t*
*Aulacomnium palustris*, 223*t*
*Avena brevis*, 475–490
*Avena fatua* (Wild Oats), 312*t*
*Avena nuda* (Naked Oats), 89*t*, 475–490
*Avena sativa* L. (Oats), 18*t*, 42*t*, 70*t*, 89*t*, 178*t*, 189*t*, 200*t*, 223*t*, 312*t*, 380*t*, 392*t*, 413*t*, 432*t*, 446*t*, 455*t*, 462*t*, 475–500
*Avena strigosa* Schreb. (Bristle Oats), 89*t*
Avens, Creeping. *See Geum reptans*
*Averrhoa carambola* (Carambola), 89*t*
*Avicennia germinans* (Black Mangrove), 200*t*, 223*t*, 312*t*
*Avicennia resinifera*, 223*t*
Avocado. *See Persea americana*; *Persea gratissima*
Ayo. *See Tetrastigma harmandii*
*Azadirachta indica* (Neem), 89*t*
*Azolla africana* (Water Fern), 89*t*
*Azolla filiculoides* (Pacific Mosquito Fern), 223*t*

**B**

Babul. *See Acacia nilotica*
*Balanites aegyptiaca* (Desert Date), 223*t*
Balsam, Garden. *See Impatiens balsamina*
Bamboo. *See Bambusa spinosa*
Bamboo, Arrow. *See Pseudosasa japonica*
Bamboo, Black. *See Phyllostachys nigra*
Bamboo, Moso. *See Phyllostachys pubescens*
Bamboo, Summer. *See Leleba oldhami*
Bamboo, Timber. *See Phyllostachys bambusoides*
*Bambusa spinosa* (Bamboo), 89*t*, 312*t*
Banana, Dwarf. *See Musa cavendishii*
*Banksia coccinea* (Scarlet Banksia), 89*t*
*Banksia hookeriana* (Hooker's Banksia), 89*t*
Baobab. *See Adansonia digitata*
Barbados Nut. *See Jatropha curcas*
*Barbarea verna* (Winter Cress), 223*t*
Barley. *See Hordeum vulgare*
Barley, Bulbous. *See Hordeum bulbosum*
Barley, Six-Rowed. *See Hordeum hexastichon*
Barley, Two-Rowed. *See Hordeum distichon*
*Bartramia halleriana* (Haller's Bartramia Moss), 223*t*
Baru. *See Dipterix alata*
*Basella rubra* (Malabar Nightshade), 89*t*
Basil. *See Ocimum basilicum*
*Bauhinia monandra* (Butterfly Flower), 89*t*
*Bauhinia purpurea* (Purple Bauhinia), 18*t*, 89*t*, 475–500
*Bauhinia variegata* (Orchid Tree), 18*t*, 89*t*, 490–500
Bayberry. *See Myrica rubra*
Bean, Adzuki. *See Vigna angularis*
Bean, Bengal. *See Stizolobium aterrimum*
Bean, Broad, Faba, Horse or Windsor. *See Vicia faba*

Bean, Bush. *See Phaseolus vulgaris* ssp. *humilis*
Bean, Castor. *See Ricinus communis*
Bean, Cluster. *See Cyamopsis tetragonolobus*
Bean, Common. *See Phaseolus vulgaris*
Bean, Common Dwarf. *See Phaseolus vulgaris* ssp. *napus*
Bean, Jack. *See Canavalia ensiformis*
Bean, Lima. *See Phaseolus lunatus*
Bean, Moth. *See Vigna aconitifolia*
Bean, Mung. *See Vigna radiata*
Bean, Negro. *See Mucuna monosperma*
Bean, Rice. *See Vigna umbellata*
Bean, Scarlet Runner. *See Phaseolus coccineus*
Bean, Small Horse. *See Vicia faba* ssp. *minor*
Bean, Tepary. *See Phaseolus acutifolius*
Bean, Velvet. *See Mucuna deeringiana*; *Mucuna pruriens*
Bean, Winged. *See Psophocarpus tetragonolobus*
Bean, Yard-Long. *See Vigna sesquipedalis*
Beech, European. *See Fagus sylvatica*
Beefwood, Cunningham. *See Casuarina cunninghamiana*
Beet, Forage. *See Beta vulgaris*, ssp *rapacea*
Beet, Sea. *See Beta maritima*
Beet, Sugar. *See Beta vulgaris*
Belladonna. *See Atropa belladonna*
Bellflower, Chinese. *See Campanula* spp
Bengal Gram. *See Cicer arietinum*
*Benincasa hispida* (Wax Gourd), 89*t*, 223*t*, 475–490
*Berlinia auriculata*, 89*t*
*Bertholletia excelsa* (Brazil Nut), 89*t*
*Beta cicla* (Swiss Chard), 223*t*
*Beta maritima* (Sea Beet), 223*t*
*Beta orientalis*, 223*t*
*Beta patellaris*, 223*t*
*Beta procumbens*, 223*t*
*Beta vulgaris* (Sugar Beet), 18*t*, 33*t*, 42*t*, 63*t*, 66*t*, 68*t*, 89*t*, 139*t*, 161*t*, 223*t*, 312*t*, 392*t*, 413*t*, 432*t*, 458*t*, 462*t*, 475–500
  *cicla* group or ssp. *cicla* (L) Koch (Spinach Beet, Swiss Chard), 223*t*
  *crassa* group or ssp. *vulgaris* (Beetroot, Sugar Beet), 223*t*
  ssp *rapacea* (Forage Beet), 18*t*, 413*t*
*Betula costata*, 312*t*
*Betula davurica*, 312*t*
*Betula ermanii*, 312*t*
*Betula nigra* (River Birch), 312*t*
*Betula papyrifera* (Paper Birch), 89*t*, 462*t*, 490–500
*Betula pendula* (European White Birch or Weeping Birch), 223*t*, 312*t*, 490–500
*Betula platyphylla* (Asian White Birch), 312*t*
*Betula pubescens* (Downy Birch), 413*t*
*Bidens pilosa* (Bur Marigold), 312*t*
*Bifora radians* (Wild Bishop), 223*t*
Birch, Asian White. *See Betula platyphylla*
Birch, Downy. *See Betula pubescens*
Birch, European White. *See Betula pendula*
Birch, Paper. *See Betula papyrifera*
Birch, River. *See Betula nigra*
Birch, Weeping. *See Betula pendula*
Birdnest Fern, Hawaii. *See Asplenium nidus*
Bird of Paradise. *See Strelitzia reginae*
Birdsfoot Trefoil. *See Lotus corniculatus*
Bishop's Weed. *See Carum copticum*
1′,3′-bis(1,2-Dilinoleoyl-*sn*-glycero-3-phospho)-*sn*-glycerol (DLDPG), 207
1′,3′-bis(1,2-Dioleoyl-*sn*-glycero-3-phospho)-*sn*-glycerol (DODPG), 206, 207
1′,3′-bis(1,2-Dipalmitoyl-*sn*-glycero-3-phospho)-1′-*sn*-glycerol (DPDPG), 206, 207, 219
1′,3′-bis(1-Stearoyl-2-oleoyl-*sn*-glycero-3-phospho)-1′-*sn*-glycerol (SODPG), 206, 207
Bitter Leaf. *See Vernonia amygdalina*
*Bixa orellana* (Annatto), 89*t*
Blackberry. *See Rubus* spp.
Bladderwort. *See Utricularia vulgaris*
*Blechnum fluviatile* (Ray Water Fern), 223*t*
*Blechnum spicant* (Deer Fern), 223*t*
*Blighia sapida* (Akee), 89*t*
Blite, Wild. *See Amaranthus blitum*; *Amaranthus lividusAmaranthus thunbergii*
Bluebell, Spanish. *See Scilla hispanica*
Bluegrass, Annual. *See Poa annua*

Bluegrass, Kentucky. *See Poa pratensis*
Bogmoss, Blandow's. *See Helodium blandowii*
Boldo. *See Peumus boldus*
Bologi, Sierra Leone. *See Crassocephalum biafrae*
*Borago officinalis* (Common Borage), 413*t*
Borecole. *See Brassica oleifera* ssp. *acephala*
Botoan. *See Musa errans*
*Bougainvillea* spp. (Bougainvillea), 223*t*
*Bouvardia ternifolia* (Firecracker Bush), 223*t*
*Brachystegia nigera* (Achi), 223*t*
*Brachythecium* spp., 223*t*
Bracken Fern. *See Pteridium aquilinum*
*Brassica campestris* (Turnip Rape), 18*t*, 33*t*, 42*t*, 78*t*, 89*t*, 200*t*, 223*t*, 312*t*, 392*t*, 475–500
ssp. *komatsuma* (Chinese Cabbage), 200*t*, 223*t*
ssp. *sarson* (Yellow Sarson), 223*t*
*Brassica carinata* (Abyssinian Mustard), 89*t*
*Brassica caulorapa* (Kohlrabi), 223*t*
*Brassica chinensis* (Pak-Choi, Chinese Mustard), 89*t*, 312*t*, 380*t*, 432*t*, 475–490
*Brassica hirta*. *See Sinapis alba*
*Brassica integrifolia* (Indian Brown Mustard), 89*t*
*Brassica juncea* (Indian Mustard), 89*t*, 223*t*, 462*t*, 475–490
*Brassica napobrassica* (Rutabaga), 89*t*
*Brassica napus* (Rape), 18*t*, 33*t*, 42*t*, 89*t*, 152*t*, 178*t*, 189*t*, 200*t*, 212*t*, 223*t*, 312*t*, 413*t*, 475–500
ssp. *oleifera* (Winter Rape), 152*t*, 212*t*, 223*t*, 312*t*, 413*t*, 475–500
*Brassica nigra* (Black Mustard), 42*t*, 223*t*, 312*t*, 413*t*
*Brassica oleracea* (Oilseed Rape), 89*t*, 152*t*, 158*t*, 178*t*, 200*t*, 212*t*, 223*t*, 312*t*, 380*t*, 392*t*, 413*t*, 446*t*, 455*t*, 462*t*, 475–500
ssp. *acephala* (Kale, Collards, Borecole), 89*t*, 223*t*
ssp. *botrytis* (Cauliflower), 89*t*, 152*t*, 158*t*, 178*t*, 212*t*, 223*t*, 312*t*, 462*t*, 475–490
ssp. *capitata* (Cabbage), 89*t*, 200*t*, 223*t*, 312*t*, 380*t*, 446*t*, 455*t*, 490–500
ssp. *caulorapa* (Kohlrabi), 312*t*
ssp. *gemmifera* (Brussels Sprouts), 89*t*, 223*t*
ssp. *italica* (Broccoli), 89*t*, 312*t*, 392*t*, 413*t*, 455*t*
*Brassica pekinensis* (Pe-tsai, Chinese Cabbage), 18*t*, 42*t*, 63*t*, 66*t*, 312*t*, 392*t*, 469*t*, 475–490
*Brassica rapa* (Turnip Rape), 18*t*, 42*t*, 63*t*, 89*t*, 223*t*, 312*t*, 392*t*, 446*t*, 469*t*
ssp. *rapa* (White Turnip), 223*t*
Brazil Nut. *See Bertholletia excelsa*
Breadfruit. *See Artocarpus altilis*
Breadfruit, African. *See Treculia africana*
Breadnut. *See Artocarpus camansi*
Breech, Bear's. *See Acanthus mollis*
Brinjal. *See Solanum melongena*
Broccoli. *See Brassica oleracea*, ssp. *italica*
*Bromus erectus* (Meadow Brome), 223*t*
*Bromus pratensis* (Brome Grass), 89*t*
Broomrape. *See Orobanche crenata*
Brussels Sprouts. *See Brassica oleracea*, ssp. *gemmifera*
*Bryonia alba* (White Bryony), 223*t*
*Bryophyllum tubiflorum* (Chandelier Plant), 392*t*, 413*t*, 469*t*
*Bryum pseudotriquetrum*, 223*t*
*Buchanania lanzan* (Almondette, Chironji), 223*t*
*Buchanania latifolia* (Chirauli Nut), 89*t*
*Buchloe dactyloides* (Buffalograss), 223*t*
Buckthorn, Sea. *See Hippophaë rhamnoides*
Buckthorn, Willow-Leaved Sea. *See Hippophaë salicifolia*
Buckwheat. *See Fagopyrum esculentum*
Buffalograss. *See Buchloe dactyloides*
Bugloss, Italian. *See Echium italicum*
Buko. *See Gnetum gnemon*
*Bulnesia bonariensis* (Jaboncillo), 89*t*
*Bulnesia schickendantzii*, 89*t*
Bulrush, Roundhead. *See Scirpus holoschoemus*
Bunya-Bunya. *See Araucaria bidwillii*
*Bupleurum rotundifolium*, 223*t*
*Butea monosperma* (Palash, Flame of the Forest), 223*t*
*Butomus umbellatus* (Flowering Rush), 223*t*
Buttercup. *See Ranunculus spp.*

Buttercup, Glacier. *See Ranunculus glacialis*
Butterfly Flower. *See Bauhinia monandra*
*Butyrospermum paradoxum* (Shea Butter Tree), 223*t*

**C**

Cabbage. *See Brassica oleracea*, ssp. *capitata*
Cabbage, Chinese. *See Brassica campestris*, ssp. *komatsuma*; *Brassica pekinensis*; *Ipomoea aquatica*
Cabbage, Kerguelen. *See Pringlea antiscorbutica*
Cabbage, Swamp. *See Ipomoea aquatica*
*Caesalpinia bonducella* (Sagargota), 223*t*
*Cajanus cajan* (Pigeon Pea), 18*t*, 89*t*, 152*t*, 475–500
Calabazilla. *See Cucurbita foetidissima*
Calabur. *See Muntingia calabura*
Calamondin. *See Citrofortunella mitis*
Calcareous Moss, Olive Green. *See Mnium marginatum*
*Calendula officinalis* (Pot Marigold), 89*t*, 223*t*
*Calliergon cordifolium*, 223*t*
*Calocedrus formosana* (Formosa Incense Cedar), 223*t*
*Caloncoba echinata*, 223*t*
*Calophyllum inophyllum* (Alexandrian Laurel), 223*t*
*Calotropis gigantea* (Madar or Mudar), 223*t*
*Caltha palustris* (Cowslip), 223*t*
*Camellia japonica* (Common Camellia), 42*t*, 223*t*, 413*t*, 432*t*, 446*t*
*Camellia sasanqua* (Sasanqua Camellia), 413*t*, 446*t*
*Camellia sinensis* (Tea), 42*t*, 68*t*, 178*t*, 189*t*, 208*t*, 223*t*, 312*t*, 392*t*, 432*t*, 446*t*, 475–490
ssp. *assamica* (Assam Tea), 312*t*, 392*t*
Camel's Thorn. *See Alhagi persarum*
cAMP. *See* Cyclic Adenosine 3′,5′-Phosphate (cAMP)
*Campanula* spp, 380*t*
*Campanulatus* spp. (Chinese Bellflower), 70*t*, 89*t*, 380*t*
*Canarium ovatum* (Pili Nut), 89*t*
*Canavalia ensiformis* (Jack Bean), 89*t*, 223*t*, 475–500
*Cannabis sativa* L. (Hemp), 89*t*, 223*t*, 312*t*, 413*t*, 475–500
*Canna indica* (Indian Shot), 70*t*
Canola. *See Brassica napus*
Caper, White Bean. *See Zygophyllum album*
*Capparia spinosa* (Caper), 223*t*
*Capparis decidua* (Ker), 89*t*
*Capsella bursapastoris* (Shepherd's Purse), 89*t*
*Capsicum annuum* (Bell Pepper, Green Pepper), 18*t*, 42*t*, 89*t*, 223*t*, 312*t*, 392*t*, 413*t*, 446*t*, 490–500
*Capsicum frutescens* (Chili Pepper), 89*t*, 223*t*
Carambola. *See Averrhoa carambola*
*Carapa procera* (African Crabwood), 89*t*
Caraway. *See Carum carvi*
Cardamom. *See Elettaria cardamomum*
*Carduus acanthoides* (Black Thistle), 89*t*
*Carduus crispus* (Curly Plumeless Thistle), 413*t*
*Carica papaya* (Papaya), 89*t*, 223*t*, 413*t*
*Carica pubescens* (Mountain Papaya), 223*t*
Carnation. *See Dianthus caryophyllus*
Carob. *See Ceratonia siliqua*
*Carpinus betulus* (European Hornbeam), 89*t*, 312*t*
Carrot. *See Daucus carota*
Carrot, Wild. *See Daucus carota*, ssp. *carota*
*Carthamus oxycantha* (Wild Safflower), 223*t*
*Carthamus tinctorius* (Safflower), 89*t*, 178*t*, 223*t*, 312*t*, 392*t*, 413*t*, 475–490
Caruel. *See Philydrella pygmaea*
*Carum carvi* (Caraway), 223*t*
*Carum copticum* (Bishop's Weed), 89*t*, 223*t*, 490–500
*Carya illinoinensis* (Pecan), 89*t*, 223*t*, 446*t*
*Carya* spp. (Hickory), 89*t*
*Caryocar coriaceum* (Piqui), 223*t*
Cashew. *See Anacardium occidentale*
Cassava. *See Manihot esculenta*
*Cassia absus* (Pig's Senna), 223*t*, 475–490
*Cassia artemisiodes* (Silver Cassia), 89*t*
*Cassia fistula* (Golden Shower), 223*t*, 475–490
*Cassia nodosa* (Jointwood), 89*t*

*Cassia occidentalis* (Coffee Senna), 223*t*, 475–490
*Cassia sericea*, 89*t*
*Cassia sieberiana* DC (Ratu, African Laburnum), 89*t*
*Cassia tora* L. (Sicklepod), 223*t*
*Castanea crenata* (Japanese Chestnut), 223*t*
*Castanea sativa* (Spanish Chestnut), 70*t*, 89*t*, 413*t*
*Castanea* spp. (Chestnut), 89*t*, 446*t*
*Casuarina cunninghamiana* (Cunningham Beefwood), 89*t*
*Casuarina littoralis* (Black She Oak), 89*t*
*Casuarina muelleriana* (Slaty She Oak), 89*t*
Catechu. *See Acacia catechu*
*Catharanthus roseus* (Madagascar Periwinkle), 5, 18*t*, 42*t*, 152*t*, 158*t*, 212*t*, 312*t*, 380*t*, 392*t*, 411, 413*t*, 472*t*, 490–500
Catjang. *See Vigna catjang*
Cattail, Common. *See Typha latifolia*
*Cattleya bowringiana* (Pine Ridge Orchid), 223*t*
*Cattleya* spp., 223*t*
Cauliflower. *See Brassica oleracea*, ssp. *botrytis*
cCMP. *See* Cyclic Cytidine 3′,5′-Phosphate (cCMP)
CDP. *See* Cytidine 5′-Diphosphate (CDP)
CDP-DG. *See* Cytidine 5′-Diphosphate Diacylglycerol (CDP-DG)
CDPG. *See* Cytidine 5′-Diphosphate Glucose (CDPG/ CDPGlc)
Cedar, Formosa Incense. *See Calocedrus formosana*
Cedar, Spanish. *See Cedrela odorata*
*Cedrela odorata* (Spanish Cedar), 89*t*
*Ceiba pentandra* (Kapok), 89*t*
Celandene. *See Chelidonium majus*
Celandene, Lesser. *See Ficaria verna*
Celery, Chinese. *See Oenanthe javanica*
Celery or Celeriac. *See Apium graveolens*
*Celosia argentea* (Cockscomb), 89*t*, 223*t*
Celtuce. *See Lactuca sativa*, ssp. *asparagina*
*Centaurea calcitrapa* (Abrepuño Colorado, Star Thistle), 89*t*
*Centaurea moschata* (Sweet Sultan), 18*t*, 490–500
*Centaurea solstitialis* (Abrepuño Amarillo, Yellow Star Thistle), 89*t*
Century Plant, Dwarf. *See Agave miradorensis*
*Ceratodon purpureus*, 223*t*
*Ceratonia siliqua* (Carob), 89*t*
*Ceratophyllum demersum* (Hornwort), 223*t*, 380*t*
*Ceratophyllum* spp. (Hornwort), 89*t*, 152*t*
*Ceratophyllum submersum*, 223*t*
*Ceratopteris thalictroides* (Water Sprite), 223*t*
cGMP. *See* Cyclic Guanosine 3′,5′-Phosphate (cGMP)
*Chaenomeles japonica* (Japanese Quince), 89*t*, 432*t*
*Chaerophyllum bulbosum* (Turnip-Rooted Chervil), 223*t*
Chamomile, Sweet False. *See Matricaria chamomilla*
Chandelier Plant. *See Bryophyllum tubiflorum*; *Kalanchoë tubiflora*
Channa. *See Cicer soongaricum*
Chard, Swiss. *See Beta cicla*
Chaulmoogra Tree. *See Hydnocarpus anthelminticus*
*Chelidonium majus* (Celandine), 413*t*
*Chenopodium album* (Lambsquarters), 89*t*, 223*t*
*Chenopodium botrys* (Jerusalem Oak), 89*t*
*Chenopodium quinoa* (Quinoa), 89*t*, 152*t*, 223*t*, 475–490
*Chenopodium rubrum* (Red Goosefoot), 223*t*, 312*t*, 392*t*, 413*t*, 475–500
Cherimoya. *See Annona cherimola*
Cherry, Bird. *See Padus racemosa*; *Prunus padus*
Cherry, Mahaleb. *See Prunus mahaleb*
Cherry, Morello. *See Prunus cerasus*
Cherry, Sargent. *See Prunus sargentii*
Cherry, Sweet. *See Prunus avium*
Cherry, Winter. *See Withania somnifera*
Chervil. *See Anthriscus cerefolium*
Chervil, Turnip-Rooted. *See Chaerophyllum bulbosum*
Chestnut. *See Castanea* spp.
Chestnut, European Horse. *See Aesculus hippocastanum*

Chestnut, Japanese. *See Castanea crenata*
Chestnut, Japanese Horse. *See Aesculus turbinata*
Chestnut, Spanish. *See Castanea sativa*
Chestnut, Water. *See Eleocharis dulcis*; *Trapa natans*
Chickpea. *See Cicer arietinum*
Chickweed. *See Stellaria media*
Chicle. *See Achras zapota*
Chicory. *See Cichorium intybus*
Chile Nut. *See Gevuina avellana*
Chinaberry. *See Melia azedarach*
*Chionochloa crassiuscula*, 462*t*
*Chionochloa pallens* (Midribbed Snow Tussock), 462*t*
Chirauli Nut. *See Buchanania latifolia*
Chironji. *See Buchanania lanzan*
*Chloris gayana* (Rhodes Grass), 18*t*, 89*t*
*Chlorophytum comosum* (Spider Plant), 432*t*
Chokeberry. *See Aronia melanocarpa*
Christmas Tree, New Zealand. *See Metrosideros excelsus*
*Chromolaena odorata* (Jack in the Bush), 89*t*
*Chrysanthemum leucanthemum* (Oxeye Daisy), 413*t*
*Chrysanthemum segetum* (Corn Marigold), 413*t*
*Chrysanthemum* spp., 312*t*
*Chrysophyllum albidum* (African Starapple), 89*t*
Chufa. *See Cyperus esculentus*
Chukai Shak. *See Rumex vesicarius*
*Cicer arietinum* (Chickpea, Bengal Gram), 18*t*, 42*t*, 89*t*, 152*t*, 223*t*, 312*t*, 380*t*, 413*t*, 432*t*, 462*t*, 475–500
*Cicer soongaricum* (Channa), 223*t*
*Cichorium intybus* (Chicory), 89*t*, 223*t*, 312*t*, 392*t*, 413*t*, 475–500
Cigar Flower. *See Cuphea lanceolata*
cIMP. *See* Cyclic Inosine 3′,5′-Phosphate (cIMP)
Cineraria, Common. *See Senecio cruentus*
Cinquefoil. *See Potentilla asiatica*
*Cistus ladanifer* (Rockrose), 223*t*
*Cistus monspelliensis* (Montpelier Cistus), 413*t*
*Citrofortunella mitis* (Calamondin), 223*t*
Citron. *See Citrus acida*; *Citrus medica*
*Citrullus colocynthis* (Colocynth), 223*t*
*Citrullus lanatus* (Watermelon), 42*t*
*Citrullus vulgaris* (Watermelon), 89*t*, 223*t*, 312*t*, 413*t*, 475–490
  ssp. *fistulosus* (Squash Melon), 223*t*
Citrumelo. *See Poncirus trifoliata* × *Citrus paradisi*
*Citrus acida* (Citron), 42*t*
*Citrus amblycarpa* (Djeroek Limoe), 200*t*
*Citrus aurantifolia* (Key Lime), 223*t*
*Citrus aurantium* (Sour Orange), 89*t*, 223*t*, 312*t*, 413*t*
*Citrus grandis* (L.) Osbeck (Pummelo, Tosa-Buntan), 200*t*, 312*t*
*Citrus hassaku* (Hassaku), 490–500
*Citrus iyo* (Iyomikan), 223*t*
*Citrus jambhiri* (Rough Lemon), 223*t*
*Citrus junos* (Yuzu), 200*t*, 223*t*, 490–500
*Citrus limettioides* (Sweet Lemon), 312*t*, 490–500
*Citrus limon* (Sour Lemon), 89*t*, 223*t*, 380*t*, 490–500
*Citrus limonia* (Lime), 312*t*
*Citrus medica* (Citron), 223*t*
*Citrus medioglobosa* (Naruto), 223*t*, 490–500
*Citrus natsudaidai* (Sour Orange), 223*t*, 312*t*, 446*t*, 490–500
*Citrus nobilis* (Tangor), 89*t*
*Citrus paradisi* × *Citrus reticulata* (Tangelo), 312*t*
*Citrus reticulata* (Tangerine), 223*t*, 312*t*
*Citrus sinensis* (Orange), 18*t*, 42*t*, 89*t*, 200*t*, 223*t*, 312*t*, 380*t*, 392*t*, 413*t*, 446*t*, 455*t*, 469*t*, 490–500
*Citrus sudachi* (Sudachi), 223*t*
*Citrus tamurana* (Hyuganatsu), 223*t*, 490–500
*Citrus unshiu* (Mandarin), 200*t*, 223*t*, 380*t*
*Citrus* × *paradisi* (Grapefruit, Pomelo), 200*t*, 223*t*, 312*t*, 413*t*
*Citrus yuko* (Yuko), 223*t*
*Cladrastis lutea* (Yellowwood), 312*t*
*Clarkia rubicund*, 223*t*
*Clianthus formosus* (Sturt Desert Pea), 89*t*

*Climacium dendroides*, 223*t*
*Climacoptera crassa*, 462*t*, 490–500
*Clitoria ternatea* (Blue Pea), 89*t*
Clover, Berseem. *See Trifolium alexandrinum*
Clover, Bush. *See Lespedeza bicolor*
Clover, Crimson. *See Trifolium incarnatum*
Clover, Hartshorn. *See Trifolium* spp.
Clover, Red. *See Trifolium pratense*
Clover, Sub. *See Trifolium subterraneum*
Clover, White. *See Trifolium repens*
Clover, White Sweet. *See Melilotus alba*
Clover, Yellow Sweet. *See Melilotus officinalis*
Clubmoss, Fir. *See Huperzia selago*
Clubmoss, Tooth-Leaved. *See Selaginella denticulata*
CMP. *See* Cytidine 5′-Phosphate (CMP)
*Cochlearia anglica* (English Scurvy Grass), 223*t*
Cocklebur. *See Xanthium strumarium*
Cocklebur, Oriental. *See Xanthium orientale*
Cockle, Cow. *See Agrostemma githago*; *Saponaria vaccaria*
Cockscomb. *See Celosia argentea*
Cocksfoot. *See Dactylis glomerata*
Cocoa. *See Theobroma cacao*
*Cocos nucifera* (Coconut), 89*t*, 152*t*, 223*t*, 380*t*, 475–490
Cocoyam. *See Xanthosoma* spp.
*Coffea arabica* (Coffee), 89*t*, 152*t*, 223*t*, 446*t*
*Coffea robusta*, 152*t*
Coigue. *See Nothofagus dombeyi*
*Coix lacryma-jobi* (Job's Tears, Adlay), 223*t*, 432*t*
*Cola acuminata* (Abata Cola), 89*t*
*Colchicum autumnale* (Autumn Crocus), 70*t*
*Coleus blumei* (Painted Nettle), 66*t*, 380*t*
*Coleus shirensis*, 312*t*
Collards. *See Brassica oleifera* ssp. *acephala*
*Colocasia antiquorum* (Egyptian Taro), 70*t*, 89*t*
*Colocasia esculenta* (Taro), 70*t*, 89*t*, 200*t*, 223*t*, 446*t*
Colocynth. *See Citrullus colocynthis*
Coltsfoot. *See Tussilago farfara*
Columbine, Alpine. *See Aquilegia alpina*
Columbine, European. *See Aquilegia vulgaris*
*Concephalum conicum* (Scented Liverwort), 223*t*
*Concephalum* spp., 7*t*
*Conium maculatum* (Poison Hemlock), 89*t*
Conophor. *See Tetracarpidium conophorum*
*Convallaria majalis* (Lily of the Valley), 223*t*
*Conyza canadensis* (Horseweed), 223*t*
Copaiba, African. *See Daniellia oliveri*
Coral Tree, Naked. *See Erythrina coralloides*
Coralwood. *See Adenanthera pavonina*
*Corchorus capsularis* (Jute), 312*t*, 475–490
*Corchorus olitorius* (Tossa Jute), 89*t*
Cordgrass, Saltmeadow. *See Spartina patens*
Cordgrass, Smooth. *See Spartina alterniflora*
*Coriandrum sativum* (Coriander), 18*t*, 42*t*, 89*t*, 223*t*, 475–490
Corn. *See Zea mays*
Corn, Dent. *See Zea mays*, ssp. *indentata*
Corn, Flint. *See Zea mays*, ssp. *indurata*
Corn, Sweet. *See Zea mays*, ssp. *saccharata*
Corylus avellana (European Hazel), 89*t*, 152*t*, 223*t*, 312*t*, 413*t*, 475–490
*Cosmos* spp. (Aster), 432*t*
*Costus speciosus* (Crepe Ginger), 312*t*, 408, 413*t*
*Cotoneaster dammeri* (Bearberry Cotoneas-ter), 37
Cotton, American Wild. *See Gossypium aridum*
Cotton, Levant. *See Gossypium herbaceum*
Cotton, Sea Island. *See Gossypium barbadense*
Cotton, Thurber's. *See Gossypium thurberi*
Cotton, Tree. *See Gossypium arboreum*
Cotton, Upland. *See Gossypium hirsutum*
Cottonwood, Eastern. *See Populus deltoides*
*Coula edulis* (Gabon Nut), 89*t*
Cow Herb. *See Vaccaria segetalis*
Cowitch. *See Mucuna pruriens*
Cowpea. *See Vigna unguiculata*
Cowpea, Hairypod. *See Vigna luteola*
Cowslip. *See Caltha palustris*
Crabapple. *See Malus sylvestris*
Crabapple, Siberian. *See Malus baccata*
Crabgrass, Hairy. *See Digitaria sanguinalis*
Crabwood, African. *See Carapa procera*
*Crambe abyssinica* (Crambe), 89*t*, 223*t*
*Crambe amabilis*, 178*t*, 223*t*, 490–500

*Crambe schugnana*, 223*t*
Cranberry. *See Vaccinium macrocarpon*
*Crassocephalum biafrae* (Sierra Leone Bologi), 89*t*
*Crassocephalum crepidioides* (Hawksbead Velvetplant), 89*t*
*Crataegus turkestanica* (Turkestan Hawthorn), 223*t*
Cress, Amphibious Marsh. *See Rorippa amphibia*
Cress, Garden. *See Lepidium sativum*
Cress, Mouse-Ear. *See Arabidopsis thaliana*
Cress, Winter. *See Barbarea verna*
Crocus, Autumn. *See Colchicum autumnale*
*Crotalaria juncea* (Sunnhemp), 223*t*
*Crotalaria retusa* (Rattleweed), 223*t*
Crystalwort. *See Riccia fluitans*
*Ctenidium molluscum* (Mollusc Ctenidium Moss), 223*t*
cTMP. *See* Cyclic Thymidine 3′,5′-Phosphate (cTMP)
CTP. *See* Cytidine 5′-Triphosphate (CTP)
Cubeb, African. *See Piper clusii*
Cubeb, Guinea. *See Piper guineense*
Cuckoopint. *See Arum maculatum*
Cucumber. *See Cucumis sativus*
Cucumber, Bur. *See Sicyos angulatus*
*Cucumis melo* (Melon), 89*t*, 223*t*, 312*t*
ssp. *reticulatus* (Muskmelon), 223*t*
*Cucumis sativus* (Cucumber), 18*t*, 42*t*, 63*t*, 89*t*, 200*t*, 223*t*, 312*t*, 380*t*, 392*t*, 413*t*, 475–500
*Cucurbita andreana* (Winter Squash), 89*t*
*Cucurbita digitata* (Squash, Coyote Gourd), 89*t*, 223*t*
*Cucurbita ficifolia* (Figleaf Gourd), 223*t*
*Cucurbita foetidissima* (Calabazilla), 89*t*, 223*t*
*Cucurbita maxima* (Hubbard Squash), 18*t*, 42*t*, 63*t*, 89*t*, 223*t*, 312*t*, 392*t*, 413*t*
*Cucurbita mixta* (Silver-Seed Gourd), 89*t*
*Cucurbita moschata* (Warty Squash), 89*t*, 200*t*, 223*t*, 475–490
*Cucurbita palmata* (Coyote Gourd), 89*t*
*Cucurbita pepo* (Pumpkin), 18*t*, 42*t*, 89*t*, 223*t*, 312*t*, 392*t*, 413*t*, 446*t*, 458*t*, 462*t*, 490–500
ssp. *melopepo* (Zucchini Squash), 223*t*
*Cucurbita* spp. (Squash), 7*t*, 446*t*
Cumin. *See Cuminum cyminum*
Cumin, Black. *See Nigella sativa*
*Cuminum cyminum* (Cumin), 89*t*, 223*t*
cUMP. *See* Cyclic Uridine 3′,5′-Phosphate (cUMP)
*Cuphea lanceolata* (Cigar Flower), 475–490
*Cupressus dupreziana* (Saharan Cypress), 223*t*
*Curcuma longa* (Turmeric), 70*t*, 89*t*
*Curcuma viridiflora*, 70*t*
Currant, Black. *See Ribes nigrum*
Curry Leaf. *See Murraya koenigii*
*Cuscuta campestris* (Cuscuta, Field Dodder), 462*t*, 475–490
*Cuscuta reflexa* (Dodder), 89*t*, 223*t*, 392*t*, 413*t*, 469*t*
*Cyamopsis psoralioides* (Cluster Bean), 89*t*
*Cycas revoluta* (Sago Palm), 446*t*
*Cycas tharwanara*, 223*t*
*Cyclamen persicum* (Cyclamen), 200*t*, 223*t*
Cyclic Adenosine 3′,5′-Phosphate (cAMP), 376
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*Cyclobalanopsis globosa*, 312*t*, 475–490
*Cydonia oblonga* (Quince), 223*t*
*Cymbidium* hybrid, 223*t*
*Cynoglossum creticum* (Blue Hound's Tongue), 89*t*
*Cynoglossum officinale* (Hound's Tongue), 223*t*
*Cyperus esculentus* (Chufa, Yellow Nutsedge), 70*t*, 89*t*, 223*t*
*Cyperus rotundus* (Purple Nutsedge), 70*t*
*Cyphomandra betacea* (Tree Tomato), 89*t*
Cypress, Saharan. *See Cupressus dupreziana*
*Cypripedium insigne* (Large-Flowered Lady's Slipper), 223*t*

Cytidine 5′-Diphosphate (CDP), 309*t*, 312*t*, 349, 359–360, 387–388, 407–408, 473*t*, 475–500
Cytidine 5′-Diphosphate Choline (CDP-Choline), 160, 160*f*, 359
Cytidine 5′-Diphosphate Diacylglycerol (CDP-DG), 9*f*, 160, 160*f*
Cytidine 5′-Diphosphate Ethanolamine (CDP-Ethanolamine), 160, 160*f*
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Cytidine 5′-Phosphate (CMP), 305, 309*t*, 312*t*, 349, 358, 359–360, 362, 369, 378, 379, 407–408, 413*t*, 437, 473*t*, 475–500
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5′-Cytidylic acid. *See* Cytidine 5′-Phosphate (CMP)

**D**

*Dactylis glomerata* (Orchard Grass, Cocksfoot), 89*t*, 223*t*
dADP. *See* 2′-Deoxyadenosine 5′-Diphosphate (dADP)
Daffodil. *See Narcissus* spp.
*Dahlia pinnata* (Dahlia), 392*t*
Daisy, Golden Everlasting. *See Helichrysum bracteatum*
Daisy, Oxeye. *See Chrysanthemum leucanthemum*
D-*altro*-2-Idooctulose 1,8-bisphosphate (Id1,8P), 65
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Dandelion. *See Taraxacum* spp.
Danggui. *See Angelica sinensis*
*Daniellia oliveri* (African Copaiba), 89*t*
Darnel. *See Lolium temulentum*
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dATP. *See* 2′-Deoxyadenosine 5′-Triphosphate (dATP)
*Datura inoxia* (Downy Thorn Apple), 223*t*, 312*t*, 392*t*, 413*t*, 490–500
*Datura* spp. (Thorn Apple), 380*t*
*Datura stramonium* (Jimsonweed), 89*t*
*Daucus carota* (Carrot), 18*t*, 42*t*, 89*t*, 152*t*, 158*t*, 178*t*, 189*t*, 200*t*, 212*t*, 218*t*, 223*t*, 312*t*, 380*t*, 392*t*, 413*t*, 432*t*, 455*t*, 490–500
ssp. *carota* (Wild Carrot, Queen Anne's Lace), 223*t*
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*Delonix regia* (Flamboyant, Royal Poinci-ana), 89*t*, 223*t*
*Dendrobium kingianum* (Pink Rock Orchid), 223*t*
*Dendrobium lowii*, 89*t*
2′-Deoxyadenosine 5′-Diphosphate (dADP), 305, 306, 363, 363*t*, 364, 365–366, 475–490
2′-Deoxyadenosine 5′-Phosphate (dAMP), 305, 306, 363, 363*t*, 364, 365–366
2′-Deoxyadenosine 5′-Triphosphate (dATP), 305, 306, 347, 363, 363*t*, 364, 365–366
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2′-Deoxyuridine 5′-Phosphate (dUMP), 305, 363, 369, 370
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*Deschampsia caespitosa* (Tufted Hairgrass), 89*t*
*Detarium microcarpum*, 89*t*
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dGDP. *See* 2′-Deoxyguanosine 5′-Diphosphate (dGDP)
dGMP. *See* 2′-Deoxyguanosine 5′-Phosphate (dGMP)
dGTP. *See* 2′-Deoxyguanosine 5′-Triphosphate (dGTP)
DHAP. *See* Dihydroxyacetone Phosphate (DHAP)
*Dianthus caryophyllus* (Carnation), 152*t*, 158*t*, 178*t*, 189*t*, 200*t*, 208*t*, 212*t*, 223*t*
*Diapensia lapponica* (Pincushion Plant), 223*t*, 490–500
*Dicranella coarctata*, 380*t*
*Dicranella heteromolla*, 223*t*
*Dicranum polysetum* (Dicranum Moss), 223*t*
*Digitalis lanata* (Grecian Foxglove), 312*t*, 409, 413*t*
*Digitalis purpurea* (Foxglove), 392*t*, 413*t*
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1,2-Dilinolenoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (DLnPI), 211
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1,2-Dilinoleoyl-*sn*-glycero-3-(dihydrogen phosphate) (DLPA), 221, 222
1,2-Dilinoleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (DLPI), 211
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*Dioscorea alata* (Winged Yam), 89*t*, 223*t*
*Dioscorea batatas* (Chinese Yam), 89*t*, 223*t*
*Dioscorea bulbifera* (Air Potato), 223*t*
*Dioscorea cayenensis* (Yellow Guinea Yam), 223*t*
*Dioscorea esculenta* (Lesser Yam), 166*t*
*Dioscorea japonica* (Japanese Yam), 223*t*
*Dioscorea opposita* (Chinese Yam), 223*t*
*Dioscorea rotundata* (White Guinea Yam), 89*t*, 223*t*

*Dioscorea versicolor* (Yam), 89*t*
*Dioscoreophyllum cumminsii* (Serendipity Berry), 89*t*
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*Diospyros discolor* (Persimmon, Mabolo), 89*t*
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1,2-Dipalmitoyl-*sn*-glycero-3-(dihydrogen phosphate) (DPPA), 205, 207, 216, 219, 220, 222
1,2-Dipalmitoyl-*sn*-glycero-3-phosphocholine (DPPC), 174, 177, 183, 185, 193, 205, 219, 222
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*Dipsacus fullonum*, var. *sylvestris* (Teasel), 89*t*
*Dipteryx alata* (Baru), 89*t*
*Diptychocarpus strictus*, 89*t*, 178*t*, 189*t*, 208*t*, 223*t*
1,2-Distearoyl-*sn*-glycero-3-phosphocholine (DSPC), 183, 185
*Distichlis spicata* (Coastal Saltgrass), 18*t*, 312*t*, 475–490
Dittany. *See Origanum dictamnus*
DLDPG. *See* 1′,3′-bis(1,2-Dilinoleoyl-*sn*-glycero-3-phospho)-*sn*-glycerol (DLDPG)
DLnPA. *See* 1,2-Dilinolenoyl-*sn* -glycero-3-(dihydrogen phosphate) (DLnPA)
DLnPC. *See* 1,2-Dilinolenoyl-*sn*-glycero-3-phosphocholine (DLnPC)
DLnPE. *See* 1,2-Dilinolenoyl-*sn*-glycero-3-phospho-1′-ethanolamine (DLnPE)
DLnPG. *See* 1,2-Dilinolenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (DLnPG)
DLnPI. *See* 1,2-Dilinolenoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (DLnPI)
DLPA. *See* 1,2-Dilinoleoyl-*sn*-glycero-3-phospho-3-(dihydrogen phosphate) (DLPA)
DLPC. *See* 1,2-Dilinoleoyl-*sn*-glycero-3-phospho-3-phosphocholine (DLPC)
DLPE. *See* 1,2-Dilinoleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (DLPE)
DLPG. *See* 1,2-Dilinoleoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (DLPG)
DLPI. *See* 1,2-Dilinoleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (DLPI)
DLPS. *See* 1,2-Dilinoleoyl-*sn*-glycero-3-phospho-L-serine (DLPS)
D-*myo*-Inositol 1,2-Bisphosphate (Ins(1,2)$P_2$), 135, 142, 143, 144
D-*myo*-Inositol 1,4-Bisphosphate (Ins(1,4)$P_2$), 135, 142, 143, 144, 215
D-*myo*-Inositol 3,4-Bisphosphate (Ins(3,4)$P_2$), 135, 143, 144
D-*myo*-Inositol 4,5-Bisphosphate (Ins(4,5)$P_2$), 135, 143, 144, 159
D-*myo*-Inositol 1,2,4,5,6-Pentakisphosphate (Ins(1,2,4,5,6)$P_5$), 135, 150, 151
D-*myo*-Inositol 1-Phosphate (Ins(1)P), 77, 135, 139, 140, 141, 142, 157

D-*myo*-Inositol 3-Phosphate (Ins(3)P), 135, 139, 140, 140*f*, 141, 142
D-*myo*-Inositol 4-Phosphate (Ins(4)P), 135, 139, 140, 141–142, 159, 172–173
D-*myo*-Inositol 1,2,3,6-Tetrakisphosphate (Ins(1,2,3,6)$P_4$), 135, 147, 148, 149
D-*myo*-Inositol 1,2,5,6-Tetrakisphosphate (Ins(1,2,5,6)$P_4$), 135, 147, 148, 149
D-*myo*-Inositol 1,3,4,5-Tetrakisphosphate (Ins(1,3,4,5)$P_4$), 135, 147*f*, 148, 149
D-*myo*-Inositol 1,4,5,6-Tetrakisphosphate (Ins(1,4,5,6)$P_4$), 135, 148, 149
D-*myo*-Inositol 3,4,5,6-Tetrakisphosphate (Ins(3,4,5,6)$P_4$), 135, 148, 149
D-*myo*-Inositol 1,2,6-Trisphosphate (Ins(1,2,6)$P_3$), 135, 145
D-*myo*-Inositol 1,4,5-Trisphosphate (Ins(1,4,5)$P_3$), 135, 138, 139*t*, 145, 146, 147*f*, 149, 215
D-*myo*-Inositol 1,5,6-Trisphosphate (Ins(1,5,6)$P_3$), 135, 145, 146
D-*myo*-Inositol 3,4,6-Trisphosphate (Ins(3,4,6)$P_3$), 135, 145, 146
Dodder. *See Cuscuta reflexa*
Dodder, Field. *See Cuscuta campestris*
DODPG. *See* 1′,3′-bis(1,2-Dioleoyl-*sn*-glycero-3-phospho)-*sn*-glycerol (DODPG)
Dog Weed, Mad. *See Alisma plantago-aquatica*
Dolichos biflorus. *See Macrotyloma uniflorum*
Dolichos lablab. *See Lablab purpureus*
DOPA. *See* 1,2-Dioleoyl-*sn*-glycero-3-(dihydrogen phosphate) (DOPA)
DOPC. *See* 1,2-Dioleoyl-*sn*-glycero-3-phosphocholine (DOPC)
DOPE. *See* 1,2-Dioleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (DOPE)
DOPG. *See* 1,2-Dioleoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (DOPG)
DOPI. *See* 1,2-Dioleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (DOPI)
DOPS. *See* 1,2-Dioleoyl-*sn*-glycero-3-phospho-L-serine (DOPS)
Dougoufoulo. *See Vouandzeia passonii*
DPDPG. *See* 1′,3′-bis(1,2-Dipalmitoyl-*sn*-glycero-3-phospho)-1′-*sn*-glycerol (DPDPG)
DPG. *See* Diphosphatidylglycerol (DPG)
1,3-DPGA. *See* 1,3-Diphosphoglyceric Acid (1,3-DPGA)
2,3-DPGA. *See* 2,3-Diphosphoglyceric Acid (2,3-DPGA)
DPPA. *See* 1,2-Dipalmitoyl-*sn*-glycero-3-(dihydrogen phosphate) (DPPA)
DPPC. *See* 1,2-Dipalmitoyl-*sn*-glycero-3-phosphocholine (DPPC)
DPPE. *See* 1,2-Dipalmitoyl-*sn*-glycero-3-phospho-1′-ethanolamine (DPPE)
DPPG. *See* 1,2-Dipalmitoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (DPPG)
DPPI. *See* 1,2-Dipalmitoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (DPPI)
DPPI(3)P. *See* 1,2-Dipalmitoyl-*sn*-glycero-3-phospho-D-*myo*-inositol 3-Phosphate (DPPI(3)P)
DPPI(3,4)$P_2$. *See* 1,2-Dipalmitoyl-*sn*-glycero-3-phospho-D-*myo*-inositol 3,4-Bisphosphate (DPPI(3,4)$P_2$)
DPPI(4)P. *See* 1,2-Dipalmitoyl-*sn*-glycero-3-phospho-D-*myo*-inositol 4-Phosphate (DPPI(4)P)
DPPI(4,5)$P_2$. *See* 1,2-Dipalmitoyl-*sn*-glycero-3-phospho-D-*myo*-inositol 4,5-Bisphosphate (DPPI(4,5)$P_2$)
DPPS. *See* 1,2-Dipalmitoyl-*sn*-glycero-3-phospho-L-serine (DPPS)
*Drepanocladus lycopodioides*, 223*t*
*Drimys lanceolata*, 312*t*, 392*t*
*Drimys lanceolata* (Pepper Tree), 312*t*, 392*t*
*Dryandra formosa* (Showy Dryandra), 89*t*
*Dryopteris dilatata*, 223*t*
*Dryopteris filix-mas* (Shield Fern), 223*t*
DSPC. *See* 1,2-Distearoyl-*sn*-glycero-3-phosphocholine (DSPC)
Duckweed. *See Spirodela oligorrhiza*
Duckweed, Giant. *See Spirodela polyrrhiza*
Duckweed, Gibbous. *See Lemna gibba*
Duckweed, Lesser. *See Lemna minor*; *Lemna paucicostata*
Duckweed, Star. *See Lemna trisulca*
dUDP. *See* 2′-Deoxyuridine 5′-Diphosphate (dUDP)

dUMP. *See* 2′-Deoxyuridine 5′-Phosphate (dUMP)
Durra, White. *See Sorghum bicolor*, var. *cernuum*
dUTP. *See* 2′-Deoxyuridine 5′-Triphosphate (dUTP)
dXu5P. *See* 1-Deoxy-D-Xylulose 5-Phosphate (dXu5P)

**E**

Ébano. *See Pithecellobium flexicaule*
*Echinochloa colona* (Barnyard Millet), 223*t*
*Echinochloa cruz-galli* (Sawa Millet) ssp. *praticola* (Barnyard Grass), 312*t*, 475–490
*Echinochloa frumentacea* (Japanese Millet), 89*t*
*Echinochloa oryzicola* (Rice Barnyard Grass), 413*t*, 475–490
*Echium italicum* (Italian Bugloss), 89*t*
*Echium plantagineum* (Salvation Jane), 178*t*, 189*t*
Editan. *See Lasianthera africana*
Eelgrass. *See Vallisneria* spp.
Efiari. *See Garcinia kola*
Efik Isun. *See Icacina manni*
*Egeria densa* (Brazilian Waterweed), 42*t*, 312*t*, 392*t*, 413*t*
Eggplant. *See Solanum melongena*
Egoma. *See Perilla frutescens*, ssp. *japonica*
*Eichhornia crassipes* (Water Hyacinth), 223*t*
Einkorn. *See Triticum monococcum*
Einkorn, Wild. *See Triticum aegilopoides*; *Triticum boeoticum*
*Elaeagnus angustifolia* (Russian Olive), 223*t*
*Elaeis guineensis* (Oil Palm), 89*t*, 223*t*, 475–490
*Elaeocarpus oblongus* (Wild Olive), 89*t*
Elder, European. *See Sambucus nigra*
Elder, Seacoast Marsh. *See Iva imbricata*
*Eleocharis dulcis* (Water Chestnut), 89*t*
Elephant's Ear. *See Enterolobium cyclocarpum*
*Elettaria cardamomum* (Cardamom), 223*t*
*Eleusine coracana* (Ragi, Finger Millet), 89*t*, 475–490
*Eleusine indica* (Goosegrass), 223*t*
Elm, Japanese. *See Ulmus davidiana* ssp. *japonica*
Elm, Wych. *See Ulmus glabra*
*Elodea canadensis* (Canadian Waterweed), 223*t*, 413*t*
*Elodea nuttallii* (Western Waterweed), 223*t*
*Elyna spicata*, 223*t*
*Emilia sonchifolia* (Red Tasselflower), 89*t*
Emmer. *See Triticum dicoccum*
Emmer, Wild. *See Triticum dicoccoides*
*Encyclia fragrans*, 223*t*
*Enterolobium cyclocarpum* (Elephant's Ear), 89*t*
*Ephedra gerardiana* (Gerard Joint Fir), 223*t*
*Epidendron radicans* (Fiery Reed Orchid), 223*t*
*Episcia reptans* (Flame Violet), 312*t*
*Equisetum arvense* (Field Horsetail), 223*t*
*Equisetum scirpoides* (Dwarf Scouring Bush), 223*t*
*Equisetum sylvaticum* (Woodland Horsetail), 223*t*
*Eriobotrya japonica* (Loquat), 223*t*
*Erodium cicutarium* (Red-Stemmed Filaree), 89*t*
*Eruca sativa* (Rocket Salad, Taramira), 223*t*
*Erysimum diffusum* (Gray Wallflower), 223*t*
*Erysimum sylvestris*, 223*t*
*Erythrina coralloides* (Naked Coral Tree), 89*t*
*Erythronium japonicum* (Katakuri), 18*t*, 33*t*, 490–500
Erythrose 4-Phosphate (E4P), 1, 6*t*, 10, 11, 28, 29, 29*t*, 30, 53, 54, 63, 64–65, 490–500
*Escholtzia californica* (California Poppy), 413*t*
Etinkane. *See Piper guineense*
*Eucalyptus deglupta* (Mindanao Gum), 89*t*
*Eucalyptus erythrocorys* (Illyarie), 89*t*
*Eucalyptus youngiana* (Ooldea Mallee), 89*t*
*Euonymus europaeus* (European Spindle Tree), 223*t*, 413*t*
*Euonymus japonica* (Japanese Spindle Tree), 223*t*
*Euphorbia hirta* (Kaka Wie Adwe), 89*t*
*Euphorbia lathyris* (Caper Spurge), 413*t*
Evening Primrose. *See Oenothera biennis*

Evening Primrose, Large-Flowered. *See Oenothera biennis*, ssp. *grandiflora*
*Evodia officinalis*, 380*t*
*Evodia rutaecarpa* (Evodia), 312*t*, 380*t*

**F**

FAD. *See* Flavin adenine nucleotide (FAD)
*Fagopyrum esculentum* (Buckwheat), 18*t*, 42*t*, 70*t*, 89*t*, 223*t*, 312*t*, 446*t*, 490–500
*Fagus sylvatica* (European Beech), 223*t*, 312*t*, 490–500
Fameflower. *See Talinum triangulare*
Fan-Palm, California. *See Washingtonia filifera*
Feathertree. *See Lysiloma watsonii*
*Feijoa sellowiana* (Feijoa), 223*t*
Fennel. *See Ferula jaeschkeana*; *Foeniculum vulgare*
Fenugreek. *See Trigonella foenum-graecum*
Fern, Bracken. *See Pteridium aquilinum*
Fern, Moss. *See Selaginella pallescens*
*Ferulago silvatica*, 223*t*
*Ferula jaeschkeana* (Fennel), 223*t*
*Ferula karataviensis*, 89*t*, 223*t*
*Ferula kelleri*, 89*t*, 223*t*
*Festuca arundinacea* (Reed Fescue), 312*t*
*Festuca pratensis* (Meadow Fescue), 223*t*, 312*t*
*Ficaria verna* (Lesser Celandine), 312*t*, 490–500
*Ficus carica* (Fig), 89*t*, 223*t*
Fiddleneck. *See Phacelia tanacetifolia*
Filaree, Red-Stemmed. *See Erodium cicutarium*
Fir, Caucasian. *See Abies nordmanniana*
Fir, Douglas. *See Pseudotsuga menziesii*
Firecracker Bush. *See Bouvardia ternifolia*
Fir, Noble. *See Abies procera*
*Fissidens taxifolius* (Fissidene Moss), 223*t*
Flamboyant. *See Delonix regia*
Flame of the Forest. *See Butea monosperma*
Flaming Katy. *See Kalanchoë blossfeldiana*
*Flaveria brownii* (Brown's Yellowtops), 413*t*
*Flaveria cronquistii* (Yellowtops), 413*t*
*Flaveria pubescens* (Yellowtops), 413*t*
*Flaveria trinervia* (Clustered Yellowtops), 413*t*
Flavin Adenine Dinucleotide (FAD), 405, 429–430, 430*f*, 431, 432*t*, 436, 437, 475–500
Flavin Mononucleotide (FMN), 405, 409, 429–430, 430*f*, 431, 432*t*, 436, 437, 438, 451*f*, 475–500
Flax. *See Linum usitatissimum*
Flowering Rush. *See Butomus umbellatus*
*Flueggea microcarpa*, 223*t*
FMN. *See* Flavin mononucleotide (FMN)
*Foeniculum vulgare* (Fennel), 89*t*, 223*t*, 475–490
*Fontinalis antipyretica* (Water Moss), 223*t*
Foxglove. *See Digitalis purpurea*
Foxglove, Grecian. *See Digitalis lanata*
Foxtail, Bristly. *See Setaria verticillata*
Foxtail, Yellow. *See Setaria glauca*
F1P. *See* Fructose 1-Phosphate (F1P)
F1,6P. *See* Fructose 1,6-Bisphosphate (F1,6P)
F2,6P. *See* Fructose 2,6-Bisphosphate (F2,6P)
F6P. *See* Fructose 6-Phosphate (F6P)
*Fragaria* spp. (Strawberry), 18*t*, 89*t*, 223*t*, 312*t*, 392*t*, 469*t*
*Fragaria vesca* (Woodland Strawberry), 42*t*, 68*t*
*Fragaria* × *anasassa*, 223*t*
*Fraxinus americana* (White Ash), 312*t*
*Fraxinus excelsior* (European Ash), 86*t*, 490–500
*Fraxinus mandshurica* ssp. *japonica* (Japanese Ash), 86*t*
Frogbit. *See Limnobium spongia*
Fructose 1,6-Bisphosphate (F1,6P), 1, 2, 4*t*, 5, 6*t*, 8, 9*f*, 10–11, 14, 17–27, 36*f*, 42*t*, 53, 54, 55, 56, 57, 58, 65, 473*t*, 475–500
Fructose 2,6-Bisphosphate (F2,6P), 1, 6*t*, 42*t*, 53, 54, 55, 56, 57, 58, 475–500
Fructose 1-Phosphate (F1P), 1, 4–5, 6*t*, 39, 42*t*, 53, 54, 55, 56, 57, 490–500
Fructose 6-Phosphate (F6P), 1, 2–3, 4–5, 4*t*, 6*t*, 8, 10, 11, 14, 17–27, 28, 29, 30, 36–37, 36*f*, 39, 40–53, 42*t*, 54, 55, 56, 57, 58, 59, 62, 64–65, 64*f*, 67, 68, 391, 457–460, 472*t*, 473*t*, 475–500
*Fuchsia* spp., 89*t*
*Fumaria hygrometrica*, 380*t*
*Fumaria vaillantii* (Earthsmoke), 223*t*

**G**
Gabon Nut. *See Coula edulis*
Galactose 1-Phosphate (Gal1P), 1, 4*t*, 36*f*, 59, 60, 61–62, 63*t*
Galactose 6-Phosphate (Gal6P), 59, 60, 61, 62, 63*t*, 473*t*
Galacturonic Acid 1-Phosphate (GalA1P), 388*f*
GalA1P. *See* Galacturonic Acid 1-Phosphate (GalA1P)
Gal1P. *See* Galactose 1-Phosphate (Gal1P)
Gal6P. *See* Galactose 6-Phosphate (Gal6P)
GAP. *See* Glycolic Acid Phosphate (GAP)
*Garcinia kola* (Efiari), 89*t*
*Garcinia mangostana* (Mangosteen), 89*t*
Garlic. *See Allium sativum*
Garlic, White. *See Allium neapolitanum*
GDP. *See* Guanosine 5′-Diphosphate (GDP)
GDPAra. *See* Guanosine 5′-Diphosphate Arabinose (GDPAra)
GDPFuc. *See* Guanosine 5′-Diphosphate Fucose (GDPFuc)
GDPG. *See* Guanosine 5′-Diphosphate Glucose (GDPG/ GDPGlc)
GDPGal. *See* Guanosine 5′-Diphosphate Galactose (GDPGal)
GDPMan. *See* Guanosine 5′-Diphosphate Mannose (GDPMan)
GDPRha. *See* Guanosine 5′-Diphosphate Rhamnose (GDPRha)
GDPRib. *See* Guanosine 5′-Diphosphate Ribose (GDPRib)
GDPXyl. *See* Guanosine 5′-Diphosphate Xylose (GDPXyl)
*Geum reptans* (Creeping Avens), 223*t*
*Gevuina avellana* (Chile Nut), 89*t*
Ginger. *See Zingiber officinale*
Ginger, Crepe. *See Costus speciosus*
Ginger, Kahili. *See Hedychium gardnerianum*
*Ginkgo biloba* (Ginkgo), 89*t*, 223*t*, 312*t*
Ginseng. *See Panax ginseng*
*Glaucium fimbrilligerum* (Sea Poppy), 89*t*, 223*t*
GlcNAc1P. *See* N-Acetylglucosamine 1-Phosphate (GlcNAc1P)
*Gleditsia triacanthos* (Honey Locust), 89*t*, 223*t*
Glory Vine, Crimson. *See Vitis coignetiae*
Glucose 1,6-Bisphosphate (G1,6P), 1, 475–490, 6*t*, 35, 36, 36*f*, 37, 38, 39, 40, 41, 42*t*, 53, 62
Glucose 1-Phosphate (G1P), 1, 2–3, 4*t*, 6*t*, 9*f*, 35, 36–37, 39–53, 42*t*, 59, 349, 391, 403, 404, 457–460, 473*t*, 475–500
Glucose 3-Phosphate (G3P), 69
Glucose 6-Phosphate (G6P), 1, 2–3, 4*t*, 5–6, 6*t*, 29, 31, 35, 36–37, 36*f*, 39–53, 42*t*, 54, 57, 58, 62, 69, 141, 346–347, 391, 406–407, 406*f*, 409*t*, 410–411, 457–460, 471, 472, 472*t*, 473*t*, 475–500
Glyceraldehyde 3-Phosphate (G3P), 9, 11
Glycerophosphoinositol (GroPIns), 135, 156, 157–158, 157*f*, 158*t*
Glycerophosphoinositol 3,4-Bisphosphate (GroPIns(3,4)$P_2$), 135, 156
Glycerophosphoinositol 4,5-Bisphosphate (GroPIns(4,5)$P_2$), 156, 157
Glycerophosphoinositol 4,5-Bisphosphate (GroPInsP2), 156, 157–158, 158*t*
Glycerophosphoinositol 3-Phosphate (GroPIns(3)P), 135, 156
Glycerophosphoinositol 4-Phosphate (GroPIns(4)P), 135, 156, 157
Glycerophosphoinositol 4-Phosphate (GroPInsP), 156, 157–158, 158*t*
α-Glycerophosphoric acid (α-GP), 1, 4*t*, 5–6, 6*t*, 8, 9, 9*f*, 10, 11, 12, 14, 15, 16–17, 18*t*, 27, 57, 160, 473*t*, 475–490
*Glycine max* (Soybean), 7*t*, 18*t*, 33*t*, 42*t*, 66*t*, 70*t*, 89*t*, 152*t*, 161*t*, 178*t*, 189*t*, 196*t*, 200*t*, 208*t*, 212*t*, 223*t*, 312*t*, 380*t*, 392*t*, 413*t*, 432*t*, 446*t*, 455*t*, 462*t*, 469*t*, 472*t*, 475–500
*Glycine soja* (Soybean), 89*t*, 413*t*
Glycolic Acid Phosphate (GAP), 1, 6–7, 6*f*, 8–9, 490–500
*Glycyrrhiza glabra* (Licorice), 89*t*
GMP. *See* Guanosine 5′-Phosphate (GMP)
*Gnetum africanum* (Afang), 89*t*
*Gnetum buchholzianum* (Joint Fir), 89*t*
*Gnetum gnemon* (Spinach Joint Fir, Buko), 89*t*

Goatgrass. *See Aegilops speltoides*
Goatgrass, Barb. *See Aegilops squarrosa*
*Goebelia pachycarpa*, 223*t*
Golden Shower. *See Cassia fistula*; *Oncidium sphacelatum*
Gooseberry, Cape. *See Physalis peruviana*
Goosefoot, Red. *See Chenopodium rubrum*
Goosegrass. *See Eleusine indica*
Gorose. *See Acer mono*
*Gossypium arboreum* (Tree Cotton), 223*t*, 312*t*, 392*t*, 413*t*, 490–500
ssp. *indicum*, 223*t*
*Gossypium aridum* (American Wild Cotton), 223*t*
*Gossypium armorianum*, 223*t*
*Gossypium barbadense* (Sea Island Cotton), 18*t*, 42*t*, 89*t*, 178*t*, 189*t*, 208*t*, 223*t*, 475–500
*Gossypium davidsonii*, 223*t*
*Gossypium gossypioides*, 223*t*
*Gossypium herbaceum* (Levant Cotton), 89*t*, 223*t*, 432*t*
*Gossypium hirsutum* L. (Upland Cotton), 18*t*, 33*t*, 42*t*, 89*t*, 152*t*, 161*t*, 178*t*, 189*t*, 196*t*, 200*t*, 208*t*, 223*t*, 312*t*, 392*t*, 413*t*, 458*t*, 462*t*, 475–500
*Gossypium klotzschianum*, 223*t*
*Gossypium raimondii*, 223*t*
*Gossypium* spp. (Cotton), 89*t*, 475–490
*Gossypium thurberi* (Thurber's Cotton), 223*t*
Gourd, Bottle. *See Lagenaria siceraria*
Gourd, Coyote. *See Cucurbita digitata*; *Cucurbita palmata*
Gourd, Figleaf. *See Cucurbita ficifolia*
Gourd, Silver-Seed. *See Cucurbita mixta*
Gourd, Snake. *See Trichosanthes anguina*
Gourd, Sponge. *See Luffa aegyptiaca*
Gourd, Wax. *See Benincasa hispida*
Goutweed. *See Aegopodium podagraria*
α-GP. *See* α-Glycerophosphoric acid (α-GP)
G1P. *See* Glucose 1-Phosphate (G1P)
G1,6P. *See* Glucose 1,6-Bisphosphate (G1,6P)
G3P. *See* Glucose 3-Phosphate (G3P); Glyceraldehyde 3-Phosphate (G3P)
G6P. *See* Glucose 6-Phosphate (G6P)
Gram, Black. *See Vigna mungo*
Gram, Green. *See Vigna radiata*
Gram, Horse. *See Macrotyloma uniflorum*
Grape. *See Vitis* spp.
Grapefruit. *See Citrusx paradisi*
Grape, Riverbank. *See Vitis riparia*
Grape, Wine. *See Vitis vinifera*
Grass, Barnyard. *See Echinochloa cruz-galli* ssp. *praticola*
Grass, Canary. *See Phalaris canariensis*
Grass, Dallis. *See Paspalum dilatatum*
Grass, English Scurvy. *See Cochlearia anglica*
Grass, Goose. *See Eleusine indica*
Grass, Johnson. *See Sorghum halepense*
Grass, Millet. *See Milium multiflorum*
Grass, Orchard. *See Dactylis glomerata*
Grass, Rhodes. *See Chloris gayana*
Grass, Rice Barnyard. *See Echinochloa oryzicola*
Grass, Turtle. *See Thalassia testudinum*
Greenbrier. *See Smilax* spp.
*Grevillea annulifera* (Prickly Plume Grevillea), 89*t*
*Grevillea leucopteris*, 89*t*
*Grewia asiatica* (Phalsa), 89*t*
*Grimmia pulvinata*, 223*t*
GroPIns. *See* Glycerophosphoinositol (GroPIns)
GroPInsP. *See* Glycerophosphoinositol 4-Phosphate (GroPInsP)
$GroPInsP_2$. *See* Glycerophosphoinositol 4,5-Bisphosphate ($GroPInsP_2$)
Groundnut. *See Arachis hypogaea*
Groundnut, Bambara. *See Vigna subterranea*
Groundnut, Kersting's. *See Kerstingiella geocarpa*
Groundsel. *See Senecio vulgaris*
GTP. *See* Guanosine 5′-Triphosphate (GTP)
Guanosine 5′-Diphosphate (GDP), 305–306, 309*t*, 312*t*, 349, 356, 357, 358, 387–388, 390, 473*t*, 475–500
Guanosine 5′-Diphosphate Arabinose (GDPAra), 392*t*

Guanosine 5′-Diphosphate Fucose (GDPFuc), 392*t*
Guanosine 5′-Diphosphate Galactose (GDPGal), 392*t*
Guanosine 5′-Diphosphate Glucose (GDPG/GDPGlc), 392*t*
Guanosine 5′-Diphosphate Mannose (GDPMan), 392*t*, 475–490
Guanosine 5′-Diphosphate Rhamnose (GDPRha), 392*t*
Guanosine 5′-Diphosphate Ribose (GDPRib), 392*t*
Guanosine 5′-Diphosphate Xylose (GDPXyl), 392*t*
Guanosine 5′-Phosphate (GMP), 305–306, 306*f*, 309*t*, 312*t*, 349, 354, 355, 356, 357, 358, 366, 378, 437, 473*t*, 475–500
Guanosine 5′-Triphosphate (GTP), 305–306, 309*t*, 312*t*, 349, 354, 355, 356, 357, 358, 362, 366, 372, 430, 473*t*, 475–500
5′-Guanylic acid. *See* Guanosine 5′-Phosphate (GMP)
Guava. *See Psidium guajava*
Guayabano. *See Annona muricata*
*Guizotia abyssinica* (Nigerseed), 89*t*
Gum Arabic Tree. *See Acacia arabica*; *Acacia senegal*
Gum, Mindanao. *See Eucalyptus deglupta*

**H**

Hair Cap Moss. *See Polytrichum juniperinum*
Hairgrass, Tufted. *See Deschampsia caespitosa*
*Hakea platysperma* (Cricket Ball Hakea), 89*t*
*Hakea victoriae*, 89*t*
*Halocnemum strobilaceum*, 223*t*
*Hancornia speciosa* (Mangaba Tree), 223*t*
Hassaku. *See Citrus hassaku*
Hawthorn, Turkestan. *See Crataegus turkestanica*
Hazel, European. *See Corylus avellana*
*Hedera helix* (English Ivy), 89*t*, 312*t*, 413*t*
Hedgenettle, Common. *See Stachys officinalis*
*Hedychium gardnerianum* (Kahili Ginger), 223*t*
*Helianthus annuus* (Sunflower), 18*t*, 33*t*, 42*t*, 89*t*, 152*t*, 161*t*, 178*t*, 212*t*, 223*t*, 312*t*, 380*t*, 392*t*, 413*t*, 432*t*, 462*t*, 475–500
*Helianthus tuberosus* (Jerusalem Artichoke), 18*t*, 42*t*, 89*t*, 223*t*, 312*t*, 380*t*, 392*t*, 413*t*, 446*t*, 455*t*, 472*t*, 490–500
*Helichrysum bracteatum* (Golden Everlasting Daisy), 89*t*
*Heliotropium lasiocarpum* (Heliotrope), 89*t*, 223*t*
*Heliotropium olgae*, 89*t*
*Helodium blandowii* (Blandow's Bogmoss), 223*t*
*Hemerocallis* spp. (Daylily), 392*t*
Hemlock. *See Conium maculatum*
Hemlock, Western. *See Tsuga heterophylla*
Hemp. *See Cannabis sativa*
Henbane. *See Hyoscyamus niger*
Heptose Phosphates, 62–65, 66*t*
*Heracleum angustisectum*, 223*t*
*Heracleum lehmannianum* (Cow Parsnip), 223*t*
*Heracleum mantegazzianum* (Giant Hogweed), 312*t*
*Heracleum sibiricum*, 223*t*
*Heracleum sosnowskii* (Cow Parsnip), 312*t*
*Heracleum sphondylium* (Hogweed), 42*t*
*Heracleum ternatum*, 223*t*
*Hevea brasiliensis* (Pará Rubber Tree), 89*t*, 223*t*, 312*t*
Hexose Phosphates, 35–62
*Hibiscus cannabinus* (Kenaf), 89*t*, 161*t*, 178*t*, 189*t*, 208*t*, 223*t*, 312*t*, 475–500
Hibiscus esculentus. *See Abelmoschus esculentus*
*Hibiscus huegelii* (Lilac Hibiscus), 89*t*
*Hibiscus rosa-sinensis* (Hibiscus), 490–500
*Hibiscus sabdariffa* (Roselle), 89*t*, 223*t*
Hickory. *See Carya* spp.
Hijiki. *See Hizikia fusiformis*
*Hippophaë rhamnoides* (Sea Buckthorn), 89*t*, 223*t*
*Hippophaë salicifolia* (Willow-Leaved Sea Buckthorn), 312*t*
*Hizikia fusiformis* (Hijiki), 432*t*

HLnPC. *See* 2-Linolenoyl-*sn*-glycero-3-phosphocholine (HLnPC)
HLPC. *See* 2-Linoleoyl-*sn*-glycero-3-phosphocholine (HLPC)
HLPE. *See* 2-Linoleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (HLPE)
Hogweed. *See Heracleum sphondylium*
Hogweed, Giant. *See Heracleum mantegazzianum*
Holly, English. *See Ilex aquifolium*
Hollyhock. *See Althaea rosea*
Honey Flower. *See Melianthus majus*
Honeysuckle. *See Lonicera nummulariifolia*
HOPA. *See* 2-Oleoyl-*sn*-glycero-3-(dihydrogen phosphate) (HOPA)
HOPC. *See* 2-Oleoyl-*sn*-glycero-3-phosphocholine (HOPC)
HOPE. *See* 2-Oleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (HOPE)
*Hordeum bulbosum* (Bulbous Barley), 89*t*
*Hordeum distichon* (Two-Rowed Barley), 18*t*, 42*t*, 223*t*, 312*t*, 475–490
  ssp *nutans*, 18*t*, 42*t*, 312*t*, 475–490
*Hordeum hexastichon* ssp *parallelum* (Six-Rowed Barley), 312*t*, 475–490
*Hordeum vulgare* (Barley), 7*t*, 8, 18*t*, 33*t*, 42*t*, 70*t*, 89*t*, 152*t*, 158*t*, 178*t*, 212*t*, 223*t*, 312*t*, 380*t*, 392*t*, 413*t*, 432*t*, 446*t*, 458*t*, 462*t*, 475–500
Hornbeam, European. *See Carpinus betulus*
Hornwort. *See Ceratophyllum demersum; Ceratophyllum* spp.
Horseradish Tree. *See Moringa oleifera*
Horsetail, Field. *See Equisetum arvense*
Horsetail, Woodland. *See Equisetum sylvaticum*
Horseweed. *See Conyza canadensis*
Hound's Tongue. *See Cynoglossum officinale*
Hound's Tongue, Blue. *See Cynoglossum creticum*
HPPA. *See* 2-Palmitoyl-*sn*-glycero-3-(dihydrogen phosphate) (HPPA)
HPPC. *See* 2-Palmitoyl-*sn*-glycero-3-phosphocholine (HPPC)
HPPE. *See* 2-Palmitoyl-*sn*-glycero-3-phospho-1′-ethanolamine (HPPE)
HSPA. *See* 2-Stearoyl-*sn*-glycero-3-(dihydrogen phosphate) (HSPA)
*Huperzia selago* (Fir Clubmoss), 223*t*
Hyacinth Bean. *See Lablab purpureus*
Hyacinth, Tassel Grape. *See Muscari comosum*
*Hyacinthus* spp. (Hyacynth), 223*t*
Hyacinth, Water. *See Eichhornia crassipes*
*Hydnocarpus anthelminticus* (Chaulmoogra Tree), 223*t*
4-hydroxy-L-threonine 4-phosphate, 451
*Hygrohypnum luridum* (Hygrohypnum Moss), 312*t*
*Hygrohypnum ochraceum*, 223*t*
*Hylocomium splendens*, 223*t*
*Hyoscyamus niger* (Henbane), 89*t*
*Hyphaene thebaica* (Doum Palm), 89*t*, 413*t*
*Hypnum cupressiforme* (Hypnum Moss), 223*t*
Hyuganatsu. *See Citrus tamurana*

## I

*Icacina manni* (Efik Isun), 89*t*
Ice Plant. *See Mesembryanthemum crystallinum*
Ichowa Dua. *See Ipomoea involucrata*
Iko. *See Ocimum viride*
*Ilex aquifolium* (English Holly), 223*t*
*Ilex paraguariensis* (Maté), 312*t*
*Illicium verum* (Star Anise), 223*t*
Illyarie. *See Eucalyptus erythrocorys*
*Impatiens balsamina* (Garden Balsam), 42*t*, 223*t*, 312*t*, 392*t*, 490–500
*Impatiens sultanii* (Sultana), 380*t*
Indian Shot. *See Canna indica*
Indigo, Bastard. *See Amorpha fruticosa*
*Indigofera enualphylla* (Indigo), 223*t*
*Indigofera glandulosa*, 223*t*
*Indigofera hirsuta* (Hairy Indigo), 223*t*
*Indigofera trifoliata* (Three-Leaf Indigo), 223*t*
Indigo, Hairy. *See Indigofera hirsuta*
Inosine 5′-Phosphate (IMP), 306, 306*f*, 355, 443, 475–490
Inosinic acid. *See* Inosine 5′-Phosphate (IMP)
$InsP_1$. *See myo*-Inositol Monophosphates ($InsP_1$)
$InsP_2$. *See myo*-Inositol Bisphosphates ($InsP_2$)

$InsP_3$. *See myo*-Inositol Trisphosphates ($InsP_3$)
$InsP_4$. *See myo*-Inositol Tetrakisphosphates ($InsP_4$)
$InsP_5$. *See myo*-Inositol Pentakisphosphates ($InsP_5$)
$InsP_6$. *See myo*-Inositol Hexakisphosphates ($InsP_6$); Phytic Acid ($InsP_6$)
Ipil-Ipil. *See Leucaena leucocephala*
*Ipomoea aquatica* (Swamp or Chinese Cabbage), 89*t*, 223*t*, 490–500
*Ipomoea asarifolia* (Ginger-Leaf Morning Glory), 89*t*
*Ipomoea batatas* (Sweet Potato), 89*t*, 200*t*, 223*t*, 312*t*, 392*t*, 432*t*, 490–500
*Ipomoea involucrata* (Iehowa Dua), 89*t*
*Ipomoea purga* (Jalap), 70*t*
*Iris* spp. (Iris), 70*t*, 223*t*
Ironweed. *See Vernonia galamensis*
*Irvingia gabonensis* (Ogbono), 223*t*
*Isoetes duriei*, 392*t*, 413*t*, 469*t*
*Isoetes muelleri* (a quillwort), 89*t*
*Isopterygium distichaceum*, 7*t*
*Iva imbricata* (Seacoast Marsh Elder), 475–490
Ivy, Boston. *See Parthenocissus tricuspidata*
Ivy, English. *See Hedera helix*
*Ixora parviflora* (Torch Tree), 223*t*
Iyomikan. *See Citrus iyo*

**J**

Jaboncillo. *See Bulnesia bonariensis*
Jackfruit. *See Artocarpus heterophyllus*
Jack in the Bush. *See Chromolaena odorata*
Jalap. *See Ipomoea purga*
Jangli Badam. *See Sterculia foetida*
Jasmine, Swiss Rock. *See Androsace helvetica*
*Jatropha curcas* (Barbados Nut), 89*t*
*Jatropha dulcis*, 89*t*
*Jatropha utilissima*, 89*t*
Jimsonweed. *See Datura stramonium*
Job's Tears. *See Coix lacryma-jobi*
Joint Fir. *See Gnetum buchholzianum*
Joint Fir, Gerard. *See Ephedra gerardiana*
Joint Fir, Spinach. *See Gnetum gnemon*
Jointwood. *See Cassia nodosa*
Jojoba. *See Simmondsia chinensis*
Joseph's Coat. *See Amaranthus tricolor*
*Juglans nigra* (Black Walnut), 89*t*
*Juglans regia* (English Walnut), 89*t*, 223*t*, 312*t*, 413*t*
Jujube. *See Ziziphus jujuba*
*Juncus roemerianus* (Needlegrass Rush), 312*t*
*Juniperus* spp. (Juniper), 7*t*
Jute. *See Corchorus capsularis*
Jute, Tossa. *See Corchorus olitorius*

**K**

Kaka Wie Adwe. *See Euphorbia hirta*
*Kalanchoë blossfeldiana* (Flaming Katy), 18*t*, 42*t*, 312*t*, 475–490
*Kalanchoë daigremontiana* (Devil's Backbone), 18*t*, 33*t*, 42*t*, 66*t*, 200*t*, 223*t*, 312*t*, 380*t*, 413*t*
*Kalanchoë tubiflora* (Chandelier Plant), 312*t*
Kale. *See Brassica oleifera* ssp. *acephala*
Kaoliang, 455
Kapok. *See Ceiba pentandra*
Karanja. *See Pongamia glabra*
Karroo Thorn. *See Acacia karroo*
Katakuri. *See Erythronium japonicum*
Kauri, Queensland. *See Agathis robusta*
Kaya Nut. *See Torreya nucifera*
Kenaf. *See Hibiscus cannabinus*
Ker. *See Capparis decidua*
*Kerstingiella geocarpa* (Kersting's Groundnut), 89*t*
Khakan. *See Salvadora oleoides*
Kharjur. *See Phoenix sylvestris*
Khesari. *See Lathyrus sativus*
Kiwi. *See Actinidia deliciosa*
Kleingrass. *See Panicum coloratum*
Knotgrass. *See Paspalum distichum*
*Koelreuteria paniculata* (Golden Rain Tree), 312*t*
Kohlrabi. *See Brassica caulorapa*; *Brassica oleracea*, ssp. *caulorapa*
Konjak. *See Amorphophallus konjac*
Korukapalli. *See Pithecellobium dulce*
Kudzu. *See Pueraria hirsuta*

**L**
*Lablab purpureus* (Hyacinth Bean), 89*t*, 223*t*, 432*t*, 475–490
Laburnum, African. *See Cassia sieberiana*
*Lactuca sativa* (Lettuce), 18*t*, 42*t*, 89*t*, 200*t*, 223*t*, 312*t*, 380*t*, 392*t*, 413*t*, 472*t*, 475–490
ssp. *asparagina* (Celtuce), 223*t*
Ladino. *See Trifolium repens*
Lady's Mantle. *See Alchemilla pentaphylla*
Lady's Slipper, Large-Flowered. *See Cypripedium insigne*
*Lagenaria siceraria* (Bottle Gourd), 89*t*
Lambsquarters. *See Chenopodium album*
*Laminaria japonica* (Brown Seaweed), 432*t*
*Lansium domesticum* (Langsat, Lansones), 89*t*
*Lantana camara*, ssp. *aculeata* (Yellow Sage), 223*t*
Larch. *See Larix decidua*; *Larix laricina*; *Larix leptolepis*; *Larix sibirica*
*Larix decidua* (European Larch), 42*t*, 63*t*, 312*t*, 392*t*, 413*t*
*Larix laricina* (Tamarack, American Larch), 89*t*, 462*t*, 490–500
*Larix leptolepis* (Japanese Larch), 446*t*
*Larix sibirica* (Siberian Larch), 223*t*, 490–500
*Lasianthera africana* (Editan), 89*t*
*Lathyrus sativus* (Grass Pea, Khesari), 42*t*, 89*t*, 223*t*
*Lathyrus tingitanus* (Tangier Pea), 89*t*
Laudanum. *See Cistus ladanifer*
*Launaea taraxacifolia* (Wild Lettuce), 89*t*
Laurel, Alexandrian. *See Calophyllum inophyllum*
Laurel, Cherry. *See Prunus laurocerasus*
*Lavandula latifolia* (Broad-Leaved Laven-der), 223*t*
*Lavandula vera* (English Lavender), 178*t*, 189*t*, 223*t*
Lead Tree. *See Leucaena leucocephala*
Lebbek Tree. *See Albizia lebbeck*
Leek. *See Allium porrum*
*Leleba oldhami* (Summer Bamboo), 312*t*, 392*t*, 413*t*
*Lemna gibba* (Gibbous Duckweed), 89*t*, 312*t*, 380*t*, 392*t*, 413*t*, 469*t*, 490–500
*Lemna major*, 392*t*
*Lemna minor* (Lesser Duckweed), 89*t*, 152*t*, 223*t*
*Lemna paucicostata* (Lesser Duckweed), 312*t*, 380*t*, 413*t*, 490–500
*Lemna* spp., 89*t*, 152*t*
*Lemna trisulca* (Star Duckweed), 223*t*
Lemon, Rough. *See Citrus jambhiri*
Lemon, Sour. *See Citrus limon*
Lemon, Sweet. *See Citrus limettioides*
*Lens culinaris* (Lentil), 18*t*, 70*t*, 89*t*, 152*t*, 312*t*, 413*t*, 462*t*, 475–490
Lentil. *See Lens culinaris*
*Lepidium sativum* (Garden Cress), 89*t*, 223*t*
*Lespedeza bicolor* (Bush Clover), 223*t*
Lettuce. *See Lactuca sativa*
Lettuce Tree. *See Pisonia alba*
Lettuce, Water. *See Pistia stratiotes*
Lettuce, Wild. *See Launaea taraxacifolia*
*Leucaena leucocephala* (Lead Tree, Ipil-Ipil), 89*t*
*Levisticum officinale* (Lovage), 223*t*
LHPA. *See* 1-Linoleoyl-*sn*-glycero-3-(dihydrogen phosphate) (LHPA)
LHPC. *See* 1-Linoleoyl-*sn*-glycero-3-phosphocholine (LHPC)
LHPE. *See* 1-Linoleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (LHPE)
LHPI. *See* 1-Linoleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (LHPI)
Licorice. *See Glycyrrhiza glabra*
Ligusticum acutilobum. *See Angelica acutiloba*
*Lilium auratum* (Golden-Rayed Lily), 413*t*, 446*t*
*Lilium henryi* (Lily), 89*t*, 312*t*, 475–490
*Lilium longiflorum* (Trumpet Lily), 89*t*, 152*t*, 178*t*, 189*t*, 208*t*, 212*t*, 223*t*, 380*t*, 413*t*, 432*t*, 446*t*, 475–490
*Lilium philippinense* (Philippine Lily), 413*t*, 446*t*
*Lilium* spp. (Lily), 446*t*
Lily, Calla. *See Zantedeschia aethiopica*
Lily, Golden-Rayed. *See Lilium auratum*
Lily of the Valley. *See Convallaria majalis*
Lily, Philippine. *See Lilium philippinense*

Lily, Red Spider. *See Lycoris radiata*
Lily, Trumpet. *See Lilium longiflorum*
Lily, Voodoo. *See Sauromatum guttatum*
Lime. *See Citrus limonia*
Lime, Key. *See Citrus aurantifolia*
Lime Zinger. *See Xanthosoma mafaffa*
*Limnanthes alba* (Meadowfoam), 223*t*, 475–490
*Limnobium spongia* (Frogbit), 223*t*
Limoe, Djeroek. *See Citrus amblycarpa*
*Lindelofia macrostyla*, 89*t*, 223*t*
*Lindelofia tschimganica*, 89*t*, 223*t*
Linden, Large-Leaved. *See Tilia platyphyllos*
1-Linolenoyl 2-palmitoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (LnPPG), 204
1-Linolenoyl-*sn*-glycero-3-(dihydrogen phosphate) (LnHPA), 222
1-Linolenoyl -*sn*-glycero-3-phosphocholine (LnHPC), 184
2-Linolenoyl-*sn*-glycero-3-phosphocholine (HLnPC), 184
1-Linolenoyl-*sn*-glycero-3-phospho-1′-ethanolamine (LnHPE), 194, 195
1-Linolenoyl-2-*trans*-3-hexadecenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (Ln(3t)PG), 168, 204
1-Linoleoyl-2-linolenoyl-*sn*-glycero-3-(dihydrogen phosphate) (LLnPA), 221
1-Linoleoyl-2-linolenoyl-*sn*-glycero-3-phosphocholine (LLnPC), 176
1-Linoleoyl-2-linolenoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (LLnPI), 211
1-Linoleoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-ethanolamine (LLnPE), 188
1-Linoleoyl-2-linolenoyl-*sn*-glycero-3-phospho-L-serine (LLnPS), 218
1-Linoleoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (LLnPG), 200*t*
1-Linoleoyl 2-palmitoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (LPPG), 204
1-Linoleoyl-*sn*-glycero-3-(dihydrogen phosphate) (LHPA), 222
1-Linoleoyl-*sn*-glycero-3-phosphocholine (LHPC), 177–183, 184, 185, 186
2-Linoleoyl-*sn*-glycero-3-phosphocholine (HLPC), 183, 184, 185, 186
1-Linoleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (LHPI), 214
1-Linoleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol 4-Phosphate (LHPI(4)P), 217
1-Linoleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (LHPE), 194, 195
2-Linoleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (HLPE), 194, 195
1-Linoleoyl-2-*trans*-3-hexadecenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (L(3t)PG), 204
Linseed. *See Linum usitatissimum*
*Linum usitatissimum* (Flax, Linseed), 89*t*, 223*t*, 312*t*, 458*t*, 462*t*, 475–500
*Liriodendron tulipifera* (Tulip Tree), 312*t*, 392*t*
Liverwort, Scented. *See Concephalum conicum*
LLnPA. *See* 1-Linoleoyl-2-linolenoyl-*sn*-glycero-3-(dihydrogen phosphate) (LLnPA)
LLnPC. *See* 1-Linoleoyl-2-linolenoyl-*sn*-glycero-3-phosphocholine (LLnPC)
LLnPE. *See* 1-Linoleoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-ethanolamine (LLnPE)
LLnPG. *See* 1-Linoleoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (LLnPG)
LLnPI. *See* 1-Linoleoyl-2-linolenoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (LLnPI)
LLnPS. *See* 1-Linoleoyl-2-linolenoyl-*sn*-glycero-3-phospho-L-serine (LLnPS)
L-*myo*-Inositol 1,2,3,4,5-Pentakisphosphate (Ins(1,2,3,4,5)P5), 150, 151
LnHPA. *See* 1-Linolenoyl-*sn*-glycero-3-(dihydrogen phosphate) (LnHPA)
LnHPC. *See* 1-Linolenoyl -*sn*-glycero-3-phosphocholine (LnHPC)
LnHPE. *See* 1-Linolenoyl-*sn*-glycero-3-phospho-1′-ethanolamine (LnHPE)
Ln(3t)PG. *See* 1-Linolenoyl-2-*trans*-3-hexadecenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (Ln(3t)PG)

LnPPG. *See* 1-Linolenoyl 2-palmitoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (LnPPG)
Locoweed. *See Oxytropis lambertii*
Locust Bean, West African. *See Parkia clappertoniana*
Locust, Black. *See Robinia pseudoacacia*
Locust, Honey. *See Gleditsia triacanthos*
*Lolium cuneatum* (Poison Ryegrass), 89*t*, 223*t*
*Lolium multiflorum* (Italian Ryegrass), 89*t*, 380*t*, 490–500
*Lolium perenne* (Perennial Ryegrass), 223*t*, 312*t*
*Lolium* spp., 89*t*
*Lolium temulentum* (Darnel), 42*t*
*Lonicera nummulariifolia* (Honeysuckle), 89*t*
*Lophira alata* (Niam Tree), 89*t*
Loquat. *See Eriobotrya japonica*
Lotus. *See Nelumbo* spp.
*Lotus corniculatus* (Birdsfoot Trefoil), 42*t*, 89*t*, 312*t*, 490–500
Lotus, Sacred. *See Nelumbo nucifera*
Lovage. *See Levisticum officinale*
Love-Lies-Bleeding. *See Amaranthus caudatus*
LPA. *See* Lysophosphatidic acid (LPA)
LPC. *See* Lysophosphatidylcholine (LPC)
LPE. *See* Lysophosphatidylethanolamine (LPE)
LPG. *See* Lysophosphatidylglycerol (LPG)
L(3t)PG. *See* 1-Linoleoyl-2-*trans*-3-hexadecenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (L(3t)PG)
LPI. *See* Lysophosphatidylinositol (LPI)
LPIP. *See* Lysophosphatidylinositol Phosphate (LPIP)
LPL. *See* Lysophospholipids (LPL)
LPPG. *See* 1-Linoleoyl 2-palmitoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (LPPG)
LPS. *See* Lysophosphatidylserine (LPS)
Lucerne. *See Medicago sativa*
*Luffa acutangula* (Angled Luffa), 89*t*
*Luffa aegyptiaca* (Sponge Gourd, Smooth Luffa), 89*t*, 200*t*, 223*t*, 413*t*
*Lupinus albus* (White Lupine), 89*t*, 152*t*, 223*t*, 413*t*, 475–490
*Lupinus angustifolius* (Blue Lupine), 89*t*, 475–490
*Lupinus arboreus* (Tree Lupine), 223*t*, 380*t*
*Lupinus atlanticus*, 89*t*
*Lupinus cosentinii*, 89*t*
*Lupinus digitatus*, 89*t*
*Lupinus hispanicus*, 89*t*
  var. *bicolor*, 89*t*
  var. *hispanicus* (Spanish Lupine), 89*t*
*Lupinus luteus* (Yellow Lupine), 89*t*, 152*t*, 223*t*, 312*t*, 413*t*, 458*t*, 475–500
*Lupinus micranthus*, 89*t*
*Lupinus mutabilis* (Tarwi), 89*t*
*Lupinus palestinus*, 89*t*
*Lupinus pilosus* (Blue Lupine), 89*t*
*Lupinus polyphyllus* (Washington Lupine), 89*t*
  *Lupinus* spp. (Lupine), 89*t*
*Lycium chinense* (Box Thorn), 312*t*
*Lycopersicon esculentum* (Tomato), 7*t*, 18*t*, 33*t*, 42*t*, 63*t*, 89*t*, 139*t*, 178*t*, 189*t*, 212*t*, 223*t*, 312*t*, 363*t*, 380*t*, 392*t*, 413*t*, 432*t*, 446*t*, 458*t*, 462*t*, 469*t*, 475–500
  ssp. *cerasiforme* (Cherry Tomato), 89*t*, 223*t*
  ssp. *eupimpinellifolium*, 223*t*
  ssp. *pruniforme*, 223*t*
*Lycopersicon hirsutum*, ssp. *glabratum* (Wild Tomato), 223*t*
*Lycopodium annotinum* (Stiff Clubmoss), 223*t*
*Lycoris incarnata*, 223*t*
*Lycoris radiata* (Red Spiderlily), 178*t*, 200*t*, 223*t*
*Lysiloma watsonii* (Feathertree), 89*t*
*Lysimachia nummularia* (Moneywort), 223*t*
Lysophosphatidic Acid (LPA), 11, 161*t*, 166*t*, 172–173, 220, 222, 223*t*, 475–490
Lysophosphatidylcholine (LPC), 161*t*, 164*t*, 166, 166*t*, 167*t*, 172–173, 174, 183–186, 223*t*, 475–500
Lysophosphatidylethanolamine (LPE), 161*t*, 164*t*, 166*t*, 167*t*, 172–173, 174, 186, 193–195, 223*t*, 475–500
Lysophosphatidylglycerol (LPG), 166, 167*t*, 172–173, 174, 197–198, 205–206, 223*t*
Lysophosphatidylinositol (LPI), 161*t*, 166*t*, 167*t*, 172–173, 174, 207, 212–214, 212*t*, 223*t*, 475–490
Lysophosphatidylinositol Phosphate (LPIP), 172–173, 207, 212*t*, 216–217

Lysophosphatidylserine (LPS), 167*t*, 172–173, 174, 217, 219–220, 223*t*
Lysophospholipids (LPL), 163–164, 164*t*, 166, 166*t*, 167*t*, 172–174, 223*t*

**M**

Mabolo. *See Diospyros discolor*
*Macadamia integrifolia* (Macadamia Nut), 89*t*
*Machilus thunbergii*, 312*t*, 475–490
*Macrotyloma uniflorum* (Horse Gram), 89*t*, 432*t*, 475–490
*Macrozamia communis*, 223*t*
Madar. *See Calotropis gigantea*
Madder. *See Rubia tinctorum*
Mad Dog Weed. *See Alisma plantago-aquatica*
*Magnolia denudata* (Yulan), 223*t*
*Magnolia grandiflora* (Southern Magnolia), 312*t*, 392*t*, 413*t*
*Magnolia kobus* ssp. borealis, 312*t*
*Magnolia soulangiana* (Japanese Magnolia), 432*t*
Maguey. *See Agave americana*
Mahogany, African. *See Afzelia africana*
Mahogany, West Indian. *See Swietenia mahogani*
Maidenhair Fern, Australian. *See Adiantum hispidulum*
Maize. *See Zea mays*
*Malabajla graveolens*, 223*t*
Mallee, Golden. *See Eucalyptus youngiana*
Mallow, Dwarf. *See Malva rotundifolia*
Mallow, Indian. *See Abutilon molle*
Mallow, Marsh. *See Althaea officinalis*
*Malus baccata* (Siberian Crabapple), 312*t*
*Malus domestica* (Apple), 18*t*, 42*t*, 70*t*, 89*t*, 152*t*, 178*t*, 223*t*, 312*t*, 392*t*, 413*t*, 455*t*, 490–500
*Malus sylvestris* (Crabapple), 18*t*, 89*t*, 223*t*, 312*t*, 392*t*, 469*t*
*Malus xiaojinensis*, 312*t*
*Malva rotundifolia* (Dwarf Mallow), 413*t*
Mandarin. *See* Citrus unshiu
*Mandragora turcomanica* (Mandrake), 223*t*
Mandrake. *See Mandragora turcomanica*
Mangaba Tree. *See Hancornia speciosa*
*Mangifera indica* (Mango), 70*t*, 89*t*, 223*t*, 380*t*, 490–500
Mango. *See Mangifera indica*
Mangosteen. *See Garcinia mangostana*
Mangrove, Black. *See Avicennia germinans*
*Manihot esculenta* (Cassava, Manioc), 70*t*, 89*t*, 223*t*
Manio. *See Podocarpus nubigenus*
Manioc. *See Manihot esculenta*
Mannoheptulose 7-Phosphate (Ma7P), 1, 62, 63, 64, 65, 66*t*
Mannose 1-Phosphate (Man1P), 1, 59, 60, 61–62, 63*t*
Mannose 6-Phosphate (Man6P), 1, 4*t*, 36*f*, 59, 59*f*, 60, 61–62, 63*t*
Maple. *See Acer* spp.
Maple, Italian. *See Acer opalus*
Maple, Korean. *See Acer pseudosieboldianum*
Maple, Norway. *See Acer platanoides*
Maple, Silver. *See Acer saccharinum*
Maple, Sycamore. *See Acer pseudoplatanus*
*Maranta arundinacea* (Arrowroot), 70*t*, 89*t*
*Marchantia berteroana*, 223*t*
*Marchantia polymorpha*, 223*t*
Marigold, Bur. *See Bidens pilosa*
Marigold, Corn. *See Chrysanthemum segetum*
Marigold, Pot. *See Calendula officinalis*
Marrow, Vegetable. *See Cucurbita pepo*
*Marsdenia latifolium* (Utasi), 89*t*
Marvel of Peru. *See Mirabilis jalapa*
Mastic Tree, Mt. Atlas. *See Pistacia atlantica*; *Pistacia mutica*
Maté: *Ilex paraguariensis*, 312*t*
*Matricaria chamomilla* (Sweet False Chamomile), 89*t*, 223*t*
*Matthiola incana* (Tenweeks Stock), 413*t*
Meadowfoam. *See Limnanthes alba*
*Medicago media*, 178*t*
*Medicago sativa* (Alfalfa, Lucerne), 18*t*, 42*t*, 89*t*, 139*t*, 152*t*, 223*t*, 312*t*, 380*t*, 392*t*, 413*t*, 455*t*, 462*t*, 475–490
*Melia azedarach* (Chinaberry), 89*t*
*Melianthus majus* (Honey Flower), 413*t*
*Melilotus alba* (White Sweet Clover), 223*t*
*Melilotus officinalis* (Yellow Sweet Clover), 89*t*

Melon. *See Cucumis melo*
Melon-Loco. *See Apodanthera undulata*
Melon, Squash. *See Citrullus vulgaris*, ssp. *fistulosus*
*Mentha arvensis* (Field Mint), 223*t*
*Mentha spicata* (Spearmint), 89*t*
*Mesembryanthemum crystallinum* (Ice Plant), 42*t*, 223*t*
Mesquite, Honey. *See Prosopis glandulosa*
Mesquite, Velvet. *See Prosopis velutina*
*Metasequoia glyptostroboides* (Dawn Redwood), 312*t*
*Metrosideros excelsus* (New Zealand Christmas Tree), 223*t*
*Metroxylon sagu* (Sago Palm), 70*t*
Michelia compressa, 312*t*, 475–490
Mignonette, Yellow. *See Reseda lutea*
Milfoil. *See Myriophyllum* spp.
Milfoil, Eurasian Water. *See Myriophyllum spicatum*
Milfoil, Water. *See Myriophyllum quitense*
*Milium multiflorum* (Millet Grass), 413*t*
Milk Vetch. *See Astragalus bisulcatus*
Milk Vetch, Chinese. *See Astragalus chinensis*
Millet. *See Pennisetum* spp.
Millet, Barnyard. *See Echinochloa colona*
Millet, Cattail. *See Pennisetum glaucum*
Millet, Finger. *See Eleusine coracana*
Millet, Foxtail or Italian. *See Setaria italica*
Millet, Japanese. *See Echinochloa frumentacea*
Millet, Kodo. *See Paspalum scrobiculatum*
Millet, Little. *See Panicum sumatrense*
Millet, Pearl. *See Pennisetum glaucum*
Millet, Proso. *See Panicum miliaceum*
Millet, Sawa. *See Echinochloa cruz-galli*
Mimosa. *See Albizia julibrissin*
*Mimosa pudica* (Shameplant), 413*t*
Mindanao Gum. *See Escholtzia californica*
Mint, Field. *See Mentha arvensis*
*Mirabilis jalapa* (Marvel of Peru), 413*t*
Mistletoe. *See Viscum album*
Mistletoe, African. *See Tapinanthus dodoneifolius*
Mkpa. *See Pterocarpus mildbraedii*
*Mnium cuspidatum*, 223*t*
*Mnium marginatum* (Olive Green Calca-reous Moss), 223*t*
*Mnium medium*, 223*t*
*Mnium undulatum*, 223*t*
*Molinia coerulea* (Purple Moorgrass), 413*t*
Mombin, Red. *See Spondias purpurea*
Mombin, Yellow. *See Spondias mombin*
*Momordica charantia* (Balsam Pear), 89*t*, 413*t*
Moneywort. *See Lysimachia nummularia*
Monkey Puzzle Tree. *See Araucaria araucana*
*Monodora ternifolia*, 89*t*
Moorgrass, Purple. *See Molinia coerulea*
*Moringa oleifera* (Horseradish Tree), 89*t*
*Moringa peregrina* (Yassar), 89*t*
Morning Glory. *See Ipomoea* spp.; *Pharbitis nil*
Morning Glory, Ginger-Leaf. *See Ipomoea asarifolia*
*Morus alba* (White Mulberry), 312*t*, 490–500
*Morus bombycis*, 312*t*
Mosquito Fern, Pacific. *See Azolla filiculoides*
*muco*-inositol Phosphates, 88
*Mucuna deeringiana* (Velvet Bean), 34–35, 89*t*
*Mucuna monosperma* (Negro Bean), 89*t*
*Mucuna pruriens* (Cowitch), 18*t*, 33*t*, 42*t*, 223*t*, 312*t*
*Mucuna sloanei* (Ukpo), 223*t*
*Mucuna utilis* (Mucuna Bean), 89*t*
Mudar. *See Calotropis gigantea*
Mulberry, White. *See Morus alba*
Mullein. *See Verbascum thapsus*
*Muntingia calabura* (Calabur), 223*t*
Murcott. *See Citrus reticulata*
*Murraya koenigii* (Curry Leaf), 89*t*, 223*t*
*Musa cavendishii* (Dwarf Banana), 18*t*, 42*t*, 392*t*
*Musa errans* (Botoan), 89*t*
*Musa* × *paradisiaca* (Plantain), 70*t*, 89*t*, 223*t*, 312*t*, 455*t*
*Muscari comosum* (Tassel Grape Hyacinth), 413*t*
Muskmelon. *See Cucumis melo*, ssp. *reticulatus*
Mustard, Abyssinian. *See Brassica carinata*
Mustard, Black. *See Brassica nigra*
Mustard, Chinese. *See Brassica chinensis*
Mustard, Indian. *See Brassica juncea*
Mustard, Indian Brown. *See Brassica integrifolia*

Mustard, White. *See Sinapis alba*
*myo*-Inositol Bisphosphates ($InsP_2$), 135*t*, 135, 136, 136*t*, 137–138, 137*t*, 142–144, 143*f*, 152*t*, 157, 158*t*, 475–500
*myo*-Inositol Hexakisphosphates ($InsP_6$), 75, 76, 85–86, 135–136, 137–138, 137*t*, 152*t*
*myo*-Inositol Monophosphates ($InsP_1$), 135–136, 136*t*, 137–138, 137*t*, 139–142, 140*f*, 152*t*, 475–490
*myo*-Inositol 1,2,3,4,6-Pentakisphosphate (Ins (1,2,3,4,6)$P_5$), 135, 150, 151
*myo*-Inositol 1,3,4,5,6-Pentakisphosphate (Ins (1,3,4,5,6)$P_5$), 76, 135, 147*f*, 149, 150, 151
*myo*-Inositol Pentakisphosphates ($InsP_5$), 10, 135, 136*t*, 137–138, 137*t*, 149–155, 150*f*, 152*t*, 475–490
*myo*-Inositol 2-Phosphate (InsP), 81–82, 135, 137–138, 139, 140*f*, 140, 142, 157–158, 475–490
*myo*-Inositol Phosphates, 1, 80–82, 83, 85–86
*myo*-Inositol Tetrakisphosphates ($InsP_4$), 135, 136, 136*t*, 137–138, 137*t*, 147–149, 147*f*, 152*t*, 475–490
*myo*-Inositol 1,2,3-Trisphosphate (Ins (1,2,3) $P_3$), 135, 144–145, 146
*myo*-Inositol Trisphosphates ($InsP_3$), 135, 136, 136*t*, 137–138, 137*t*, 144–147, 145*f*, 152*t*, 157, 215, 473*t*, 475–500
Myriad Leaf:. *See Myriophyllum verticillatum*
*Myrica rubra* (Bayberry), 223*t*
*Myriophyllum quitense* (Water Milfoil), 152*t*, 223*t*, 490–500
*Myriophyllum spicatum* (Eurasian Water Milfoil), 223*t*
*Myriophyllum* spp. (Milfoil), 89*t*, 152*t*
*Myriophyllum verticillatum* (Myriad Leaf), 223*t*
*Myristica fragrans* (Nutmeg), 89*t*
Myrtle, Downy. *See Rhodomyrtus tomentosa*

**N**

NAAD. *See* Nicotinic acid adenine dinucleotide (NAAD)
N-Acetylglucosamine 1-Phosphate (GlcNAc1P), 390
N-Acyllysophosphatidylethanolamine (NALPE), 161*t*, 164*t*, 166, 167*t*, 172–173, 174, 186, 195, 223*t*, 475–500
N-Acylphosphatidylethanolamine (NAPE), 159, 186, 195–197, 196*t*
NAD. *See* Nicotine Adenine Dinucleotide (NAD)
NADH. *See* Nicotine Adenine Dinucleotide, Reduced (NADH)
NADP. *See* Nicotine Adenine Dinucleotide Phosphate(NADP)
NADPH. *See* Nicotine Adenine Dinucleotide Phosphate, Reduced (NADPH)
*Najas flexilis* (Water Nymph), 380*t*
NALPE. *See* N-Acyllysophosphatidylethanolamine (NALPE)
NAMN. *See* Nicotinic acid mononucleotide (NAMN)
NAPE. *See* N-Acylphosphatidylethanolamine (NAPE)
*Narcissus* spp. (Daffodil), 223*t*
Naruto. *See Citrus medioglobosa*
Nashi. *See Pyrus pyrifolia* ssp. *culta*
*Nasturtium officinale* (Watercress), 89*t*, 223*t*
NDP. *See* Nucleoside Diphosphates (NDP)
Nectarine. *See Prunus persica*, ssp. *nectarina*
Neem. *See Azadirachta indica*
*Nelumbo nucifera* (Sacred Lotus), 70*t*, 223*t*, 413*t*
*Nelumbo* spp. (Lotus), 89*t*
*Neolitsea parvigemma*, 312*t*, 475–490
*Nerium oleander* (Oleander), 200*t*, 223*t*
Nettle, Painted. *See Coleus blumei*
Nettle, Stinging. *See Urtica dioica*
Niam Tree. *See Lophira alata*
*Nicotiana alata* (Jasmine Tobacco), 392*t*
*Nicotiana glutinosa*, 223*t*, 312*t*, 380*t*, 413*t*
*Nicotiana langsdorffii*, 490–500
*Nicotiana longiflora* (Longflower Tobacco), 413*t*
*Nicotiana quadrivalvis* (Nonchaw), 223*t*
*Nicotiana rustica* (Aztec Tobacco), 223*t*
*Nicotiana suaveolens*, 380*t*, 490–500
*Nicotiana sylvestris* (Woodland Tobacco), 18*t*, 33*t*, 223*t*, 475–490

*Nicotiana tabacum* (Tobacco), 7*t*, 18*t*, 42*t*, 152*t*, 158*t*, 178*t*, 189*t*, 200*t*, 208*t*, 212*t*, 223*t*, 312*t*, 363*t*, 380*t*, 392*t*, 413*t*, 432*t*, 462*t*, 469*t*, 472*t*, 475–500
Nicotine Adenine Dinucleotide (NAD), 5, 9*f*, 17–27, 34, 306*f*, 311, 312*t*, 346, 347, 391, 405, 406–411, 406*f*, 409*t*, 412, 413*t*, 414, 427–428, 429, 472*t*, 473*t*, 475–500
Nicotine Adenine Dinucleotide Phosphate (NADP), 5, 30, 30*f*, 36*f*, 41, 53, 57, 311, 346–347, 391, 405, 406–409, 406*f*, 410–411, 412, 413*t*, 426, 427, 428, 429, 451*f*, 473*t*, 475–500
Nicotine Adenine Dinucleotide Phosphate, Reduced (NADPH), 6*t*, 30, 306*f*, 307*f*, 346–347, 406–409, 409*t*, 410–411, 412, 413*t*, 427, 428, 429–430, 475–500
Nicotine Adenine Dinucleotide, Reduced (NADH), 6, 9*f*, 10, 11, 17–28, 34, 57, 347, 406–409, 410–411, 412, 413*t*, 426, 427, 428, 429–430, 475–500
Nicotine Mononucleotide (NMN), 413*t*, 427–428, 475–490
Nicotinic Acid Adenine Dinucleotide (NAAD), 406–407, 490–500
Nicotinic Acid Mononucleotide (NAMN), 406–407
*Nigella sativa* (Black Cumin), 223*t*
Nigerseed. *See Guizotia abyssinica*
Nightshade. *See Solanum demissum*; *Solanum phureja*
Nightshade, Black. *See Solanum nigrum*
Nightshade, Commerson's. *See Solanum commersonii*
Nightshade, Earleaf. *See Solanum mauritianum*
Nightshade, Malabar. *See Basella rubra*
*Nitraria komarovii*, 89*t*, 223*t*
*Nitraria schoberi*, 89*t*, 223*t*
NMN. *See* Nicotine Mononucleotide (NMN)
NMP. *See* Nucleoside Monophosphates(NMP)
Nonchaw. *See Nicotiana quadrivalvis*
Nori. *See Porphyra tenera*
*Nothofagus dombeyi* (Coigue), 223*t*
NTP. *See* Nucleoside Triphosphates (NTP)
Nucleoside diphosphates (NDP), 312*t*, 347, 472*t*
Nucleoside monophosphates (NMP), 312*t*, 347, 372*f*, 378, 390
Nucleoside triphosphates (NTP), 311, 312*t*, 346, 349, 472*t*, 490–500
Nucleotides, 2, 305–306, 307–311, 312*t*, 346, 349, 350, 354, 373, 374, 375, 387–388, 389, 390, 391, 392*t*, 403, 407–408, 429–430, 457, 468, 471, 473*t*
*Nuphar advena* (Spatterdock), 380*t*
*Nuphar luteum* (Yellow Water Lily), 223*t*
Nutmeg. *See Myristica fragrans*
Nutsedge, Purple. *See Cyperus rotundus*
Nutsedge, Yellow. *See Cyperus esculentus*
*Nymphoides alba*, 223*t*

**O**

Oak. *See Quercus* spp.
Oak, Durmast. *See Quercus petraea*
Oak, English. *See Quercus robur*
Oak, Jerusalem. *See Chenopodium botrys*
Oak, Northern Red. *See Quercus rubra*
Oak, Pin. *See Quercus palustris*
Oak, Portuguese. *See Quercus lusitanica*
Oak, Red:. *See Quercus borealis*
Oak, Willow. *See Quercus phellos*
Oats. *See Avena sativa*
Oats, Bristle. *See Avena strigosa*
Oats, Naked. *See Avena nuda*
Oats, Sea. *See Uniola paniculata*
Oats, Wild. *See Avena fatua*
*Ocimum basilicum* (Basil), 89*t*, 223*t*
*Ocimum viride* (Iko), 89*t*
Octose phosphates, 65–66
*Oenanthe javanica* (Chinese Celery), 392*t*
*Oenothera biennis* (Evening Primrose), 223*t*, 432*t*, 475–490
  ssp. *grandiflora* (Large-Flowered Evening Primrose), 432*t*
*Oenothera striata*, 89*t*
Ogbono. *See Irvingia gabonensis*
OHPA. *See* 1-Oleoyl-*sn*-glycero-3-(dihydrogen phosphate) (OHPA)

OHPC. *See* 1-Oleoyl-*sn*-glycero-3-phosphocholine (OHPC)
OHPE. *See* 1-Oleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (OHPE)
OHPG. *See* 1-Oleoyl-*sn*-glycero-3-phospho-*sn*-1′-glycerol (OHPG)
OHPS. *See* 1-Oleoyl-*sn*-glycero-3-phospho-L-serine (OHPS)
Oil Bean, African. *See Pentaclethra macrophylla*
Okra. *See Abelmoschus esculentus*
*Olea europaea* (Olive), 223*t*, 475–490
Oleander. *See Nerium oleander*
Oleander, Yellow. *See Thevetia neriifolia*
1-Oleoyl-2-linolenoyl-*sn*-glycero-3-phosphocholine (OLnPC), 176
1-Oleoyl-2-linolenoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (OLnPI), 211
1-Oleoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-ethanolamine (OLnPE), 188
1-Oleoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (OLnPG), 200*t*
1-Oleoyl-2-linoleoyl-*sn*-glycero-3-phosphocholine (OLPC), 176, 177
1-Oleoyl-2-linoleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (OLPI), 211
1-Oleoyl-2-linoleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (OLPE), 187, 188, 192
1-Oleoyl-2-linoleoyl-*sn*-glycero-3-phospho-L-serine (OLPS), 218, 219
1-Oleoyl-2-linoleoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (OLPG), 200*t*
1-Oleoyl-2-palmitoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (OPPG), 201, 204, 205
1-Oleoyl-*sn*-glycero-3-(dihydrogen phosphate) (OHPA), 221, 222
2-Oleoyl-*sn*-glycero-3-(dihydrogen phosphate) (HOPA), 221, 222
1-Oleoyl-*sn*-glycero-3-phosphocholine (OHPC), 183, 184, 185
2-Oleoyl-*sn*-glycero-3-phosphocholine (HOPC), 183, 184, 185
1-Oleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (OHPE), 193, 194
2-Oleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (HOPE), 194
1-Oleoyl-*sn*-glycero-3-phospho-L-serine (OHPS), 219, 220
1-Oleoyl-*sn*-glycero-3-phospho-*sn*-1′-glycerol (OHPG), 206
1-Oleoyl-2-*trans*-3-hexadecenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (O(3t)PG), 204
Olive. *See Olea europaea*
Olive, Russian. *See Elaeagnus angustifolia*
Olive, Wild. *See Elaeocarpus oblongus*
OLnPC. *See* 1-Oleoyl-2-linolenoyl-*sn*-glycero-3-phosphocholine (OLnPC)
OLnPE. *See* 1-Oleoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-ethanolamine (OLnPE)
OLnPG. *See* 1-Oleoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (OLnPG)
OLnPI. *See* 1-Oleoyl-2-linolenoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (OLnPI)
OLPC. *See* 1-Oleoyl-2-linoleoyl-*sn*-glycero-3-phosphocholine (OLPC)
OLPE. *See* 1-Oleoyl-2-linoleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (OLPE)
OLPG. *See* 1-Oleoyl-2-linoleoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (OLPG)
OLPI. *See* 1-Oleoyl-2-linoleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (OLPI)
OLPS. *See* 1-Oleoyl-2-linoleoyl-*sn*-glycero-3-phospho-L-serine (OLPS)
OMP. *See* Orotidine 5′-Phosphate (OMP)
*Oncidium sphacelatum* (Golden Shower), 223*t*
Onion. *See Allium cepa*
Onion, Welsh. *See Allium fistulosum*
*Onopordon acanthium* (Scotch Thistle), 89*t*, 223*t*
*Onopordon olgae*, 89*t*, 223*t*
O(3t)PG. *See* 1-Oleoyl-2-*trans*-3-hexadecenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (O(3t)PG)
*Ophioglossum lusitanicum* (Least Adders-tongue), 392*t*, 413*t*, 469*t*
*Ophioglossum vulgatum* (Southern Adders-tongue), 223*t*, 392*t*, 413*t*, 469*t*

OPPG. *See* 1-Oleoyl-2-palmitoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (OPPG)
Orach, Spreading. *See Atriplex patula*
Orange. *See Citrus sinensis*
Orange, Pineapple. *See Citrus sinensis*
Orange, Shamouti. *See Citrus sinensis*
Orange, Sour. *See Citrus aurantium*; *Citrus natsudaidai*
Oranguma. *See Citrus sinensis*
Orchid, Fiery Reed. *See Epidendron radicans*
Orchid, Pine Ridge. *See Cattleya bowringiana*
Orchid, Pink Rock. *See Dendrobium kingianum*
Orchid Tree. *See Bauhinia variegata*
*Oreodoxa regia* (Cuban Royal Palm), 223*t*
*Origanum dictamnus* (Dittany), 223*t*
*Orobanche crenata* (Broomrape), 223*t*
Orotidine 5′-Phosphate (OMP), 306–307
*Oryza sativa* (Rice), 7*t*, 18*t*, 42*t*, 70*t*, 78, 86, 89*t*, 135, 140, 152*t*, 161*t*, 172–173, 178*t*, 189*t*, 208*t*, 223*t*, 311, 312*t*, 380*t*, 392*t*, 413*t*, 432*t*, 446*t*, 450–451, 455, 455*t*, 457, 458*t*, 462*t*, 475–500
*Oxalis purpurata*, 70*t*
*Oxytropis lambertii* (Locoweed), 89*t*

**P**

PA. *See* Phosphatidic Acid (PA)
*Pachyrhizus erosus* (Yambean), 89*t*
Padauk, African. *See Pterocarpus osun*
*Padus racemosa* (Bird Cherry), 89*t*, 490–500
*Paeonia albiflora* (Chinese Peony), 413*t*, 446*t*
*Paeonia decora* (Peony), 223*t*
Pagoda Tree, Japanese. *See Sophora japonica*
Pak-Choi. *See Brassica chinensis*
Palash. *See Butea monosperma*
*Palisota barteri*, 223*t*
Palm, California Fan. *See Washingtonia filifera*
Palm, Cuban Royal. *See Oreodoxa regia*
Palm, Date. *See Phoenix dactylifera*
Palm, Doum. *See Hyphaena thebaica*
1-Palmitoyl-2-linolenoyl-*sn*-glycero-3-(dihydrogen phosphate) (PLnPA), 221
1-Palmitoyl-2-linolenoyl-*sn*-glycero-3-phosphocholine (PLnPC), 175, 177
1-Palmitoyl-2-linolenoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (PLnPI), 210
1-Palmitoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-ethanolamine (PLnPE), 187, 192
1-Palmitoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (PLnPG), 200*t*
1-Palmitoyl-2-linoleoyl-*sn*-glycero-3-(dihydrogen phosphate) (PLPA), 221, 222
1-Palmitoyl-2-linoleoyl-*sn*-glycero-3-phosphocholine (PLPC), 175, 177, 192, 219
1-Palmitoyl-2-linoleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (PLPI), 210, 211–212
1-Palmitoyl-2-linoleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (PLPE), 187, 192
1-Palmitoyl-2-linoleoyl-*sn*-glycero-3-phospho-L-serine (PLPS), 217, 219
1-Palmitoyl-2-linoleoyl-*sn*-glycero-3-phospho-1′*sn*-glycerol (PLPG), 200*t*
1-Palmitoyl-2-oleoyl-*sn*-glycero-3-(dihydrogen phosphate) (POPA), 220, 222
1-Palmitoyl-2-oleoyl-*sn*-glycero-3-phosphocholine (POPC), 174, 177, 183, 185, 189–192, 222
1-Palmitoyl-2-oleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (POPI), 210, 211–212
1-Palmitoyl-2-oleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (POPE), 186, 189–192
1-Palmitoyl-2-oleoyl-*sn*-glycero-3-phospho-L-serine (POPS), 217, 219
1-Palmitoyl-2-oleoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (POPG), 200*t*
1-Palmitoyl-*sn*-glycero-3-(dihydrogen phosphate) (PHPA), 185, 222
2-Palmitoyl-*sn*-glycero-3-(dihydrogen phosphate) (HPPA), 222
1-Palmitoyl-*sn*-glycero-3-phosphocholine (PHPC), 183, 185–186
2-Palmitoyl-*sn*-glycero-3-phosphocholine (HPPC), 183, 185–186

1-Palmitoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (PHPI), 211–212, 214
1-Palmitoyl-*sn*-glycero-3-phospho-D-*myo*-inositol 4-Phosphate (PHPI(4)P), 216
1-Palmitoyl-*sn*-glycero-3-phospho-1′-ethanolamine (PHPE), 193, 194
2-Palmitoyl-*sn*-glycero-3-phospho-1′-ethanolamine (HPPE), 193, 194
1-Palmitoyl-*sn*-glycero-3-phospho-L-serine (PHPS), 219, 220
1-Palmitoyl-*sn*-glycero-3-phospho-*sn*-1′-glycerol (PHPG), 205, 206
1-Palmitoyl-2-*trans*-3-hexadecenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (P(3t)PG), 199
Palm, Ivory Coast Raffia. *See Raphia hookeri*
Palm, Oil. *See Elaeis guineensis*
Palm, Raffia. *See Raphia farinifera*
Palm, Sago. *See Cycas revolutaMetroxylon sagu*
Palm, Sugar. *See Arenga pinnata*
Palm, Wild Date. *See Phoenix sylvestris*
Palm, Wine. *See Raphia vinifera*
Palo Verde, Mexican. *See Parkinsonia aculeata*
*Panax ginseng* (Ginseng), 223*t*, 380*t*
*Panicum coloratum* (Kleingrass), 18*t*
*Panicum dichotomiflorum* (Fall Panicum), 223*t*
*Panicum hemitomon*, 413*t*
*Panicum miliaceum* (Proso Millet), 70*t*, 89*t*, 223*t*, 312*t*
*Panicum sumatrense* (Little Millet), 89*t*, 223*t*
Pansy, Field. *See Viola tricolor*
*Papaver dubium* (Field Poppy), 223*t*, 475–490
*Papaver orientale* (Oriental Poppy), 413*t*, 446*t*
*Papaver rhoeas* (Corn Poppy), 139*t*
*Papaver somniferum* (Opium Poppy), 223*t*, 446*t*, 475–490
Papaya. *See Carica papaya*
Papaya, Mountain. *See Carica pubescens*
*Parkia clappertoniana* (West African Locust Bean), 89*t*
*Parkinsonia aculeata* (Mexican Palo Verde), 89*t*, 223*t*
Parsley. *See Petroselinum crispum*
Parsley, Stone. *See Sison amomum*
Parsnip. *See Pastinaca sativa*
Parsnip, Cow. *See Heracleum lehmannianum*; *Heracleum sosnowskii*
*Parthenocissus tricuspidata* (Boston Ivy), 223*t*
*Paspalum dilatatum* (Dallis Grass), 223*t*
*Paspalum distichum* (Knotgrass), 223*t*
*Paspalum scrobiculatum* (Kodo Millet, Varagu), 89*t*, 223*t*
*Pastinaca hirsuta*, 223*t*
*Pastinaca sativa* (Parsnip), 70*t*, 89*t*, 223*t*
Pasture Grass, 462*t*
PC. *See* Phosphatidylcholine (PC)
PE. *See* Phosphatidylethanolamine (PE)
Pea. *See Pisum sativum*
Pea, Blue. *See Clitoria ternatea*
Peach. *See Prunus persica*
Pea, Grass. *See Lathyrus sativus*
Peanut. *See Arachis hypogaea*
Peanut, Spanish. *See Arachis hypogaea*, ssp. *fastigiata*
Peanut, Virginia. *See Arachis hypogaea*, ssp. *hypogaea*
Pear. *See Pyrus communis*
Pear, Balsam. *See Momordica charantia*
Pear, Japanese. *See Pyrus serotina*
Pea, Sturt Desert. *See Clianthus formosus*
Pea, Tangier. *See Lathyrus tingitanus*
Pea, Zombi. *See Vigna vexillata*
Pecan. *See Carya illinoinensis*
*Peganum harmala* (African Rue), 89*t*, 223*t*
*Pellia neesiana* (Ring Pellia), 223*t*
*Pennisetum glaucum* (Pearl or Cattail Millet), 70*t*, 89*t*, 223*t*, 475–490
*Pennisetum* spp. (Millet), 89*t*, 455*t*
*Penstemon speciosus*, 223*t*
*Pentaclethra macrophylla* (African Oil Bean), 89*t*, 223*t*
Pentose Phosphates, 29–35, 30*f*, 33*t*
Peony. *See Paeonia decora*
Peony, Chinese. *See Paeonia albiflora*
Pepper, Bell. *See Capsicum annuum*
Pepper, Black. *See Piper nigrum*
Pepper, Chili. *See Capsicum frutescens*
Pepper, Green. *See Capsicum annuum*
Pepper, Guinea. *See Xylopia aethiopica*
Pepper Tree. *See Drimys lanceolata*

*Perilla frutescens* (Perilla Mint), 89*t*, 189*t*, 223*t*, 475–490
ssp. *japonica* (Egoma), 475–490
Periwinkle. *See Vinca erecta*; *Vinca minor*
Periwinkle, Madagascar. *See Catharanthus roseus*
*Persea americana* (Avocado), 18*t*, 42*t*, 89*t*, 223*t*, 312*t*, 380*t*, 413*t*, 446*t*, 469*t*, 490–500
*Persea gratissima* (Avocado), 7*t*, 42*t*, 66*t*
Persimmon. *See Diospyros discolor*
Persimmon, Japanese. *See Diospyros kaki*
*Petroselinum crispum* (Parsley), 89*t*, 212*t*, 223*t*, 380*t*, 392*t*, 413*t*, 458*t*, 475–490
Pe-Tsai. *See Brassica pekinensis*
*Petunia hybrida* (Garden Petunia), 89*t*, 212*t*, 223*t*, 475–500
*Peucedanum graveolens*. *See Anethum graveolens*
*Peucedanum verticillare*, 212*t*
*Peumus boldus* (Boldo), 413*t*
PG. *See* Phosphatidylglycerol (PG)
6-PG. *See* 6-Phosphogluconic Acid (6-PG)
2-PGA. *See* 2-Phosphoglyceric Acid (2-PGA)
3-PGA. *See* 3-Phosphoglyceric Acid (3-PGA)
*Phacelia tanacetifolia* (Fiddleneck), 312*t*, 392*t*, 413*t*, 475–490
*Phalaris canariensis* (Canary Grass), 70*t*
Phalsa. *See Grewia asiatica*
*Pharbitis nil* (Morning Glory), 223*t*, 312*t*, 413*t*, 446*t*
*Phaseolus acutifolius* (Tepary Bean), 89*t*
*Phaseolus coccineus* (Scarlet Runner Bean), 42*t*, 89*t*, 178*t*, 189*t*, 196*t*, 200*t*, 208*t*, 223*t*, 413*t*, 432*t*, 475–490
*Phaseolus lunatus* (Lima Bean), 70*t*, 89*t*, 152*t*, 223*t*, 455*t*, 475–490
*Phaseolus vulgaris* (Common Bean), 18*t*, 33*t*, 42*t*, 70*t*, 89*t*, 152*t*, 223*t*, 312*t*, 373, 380*t*, 392*t*, 413*t*, 432*t*, 455*t*, 462*t*, 475–490
ssp. *humilis* (Bush Bean), 223*t*
ssp *napus* (Dwarf Common Bean), 312*t*, 380*t*, 413*t*
*Phellodendron wilsonii* (Amur Cork Tree), 312*t*, 475–490
*Philonotis fontana*, 223*t*
*Philydrella pygmaea*, 223*t*
*Phlomis fruticosa* (Shrubby Jerusalem Sage), 413*t*
*Phoenix dactylifera* (Date Palm), 89*t*, 223*t*, 413*t*
*Phoenix sylvestris* (Wild Date Palm, Khar-jur), 223*t*
Phosphatides, 156, 460–461
Phosphatidic Acid (PA), 159, 160, 161*t*, 162–163, 164*t*, 165, 166, 166*t*, 167*t*, 170, 198–199, 220–222, 223*t*, 473*t*, 475–500
Phosphatidylcholine (PC), 159–160, 174–183, 178*t*, 475–500
Phosphatidylethanolamine (PE), 159–160, 160*f*, 186–193, 189*t*
Phosphatidylglycerol (PG), 11, 41–53, 57, 62, 159–160, 161*t*, 162, 164*t*, 165, 166, 166*t*, 167*t*, 168–169, 168*t*, 170–171, 178*t*, 197, 198–205, 200*t*, 206, 223*t*, 473*t*, 475–500
Phosphatidylinositol (PI), 86, 135, 136, 140*f*, 141, 156, 157–158, 159–160, 161*t*, 164*t*, 165, 166, 166*t*, 167*t*, 168, 170–171, 172*t*, 198–199, 207–209, 208*t*, 210–212, 212*t*, 214–215, 223*t*, 473*t*, 475–500
Phosphatidylinositol Bisphosphate ($PIP_2$), 156, 157–158, 159–160, 166, 207, 212*t*, 214–215, 216, 475–490
Phosphatidylinositol Phosphate (PIP), 156, 157–158, 159–160, 166, 207, 212*t*, 214–216, 475–490
Phosphatidylserine (PS), 159, 160, 164*t*, 165, 166, 167*t*, 168, 170, 198–199, 217–219, 223*t*, 473*t*, 475–500
Phosphocholine, 160
Phosphodextrin, 69
Phosphoenolpyruvic Acid (PEP), 2, 4*t*, 5, 6*t*, 9, 9*f*, 10–11, 13, 14, 16–17, 18*t*, 27, 61, 346–348, 349, 357, 360, 362, 380, 457–460, 473*t*, 475–500
Phosphoethanolamine, 160
6-Phosphogluconic Acid (6-PG), 1, 4*t*, 5–6, 6*t*, 30, 30*f*, 31, 35, 36–37, 36*f*, 38, 40, 41, 42*t*, 53, 57, 473*t*, 475–500

2-Phosphoglyceric Acid (2-PGA), 1, 4*t*, 6*t*, 9, 10–11, 12, 14, 15–17, 18*t*, 27, 490–500
3-Phosphoglyceric Acid (3-PGA), 1, 2, 4*t*, 5, 6–7, 6*t*, 8–9, 9*f*, 10–11, 12, 13, 14, 15–17, 18*t*, 27, 34, 57, 475–500
Phospholipids (PL), 2, 159–304, 460, 471, 473*t*
Phosphoproteins, 460
Phosphoric Acid (Pi), 2, 3, 4, 4*t*, 5, 8–9, 11, 14, 15, 16, 40–41, 56, 57, 59, 61–62, 63, 76, 84–86, 86*t*, 135, 142, 152*t*, 157, 168, 212*t*, 214, 217, 218*t*, 309*t*, 311, 354–355, 357, 358, 360, 362–363, 379, 380, 438, 453, 457–468, 458*t*, 462*t*, 469*t*, 471, 472, 472*t*, 473*t*, 475–500
Phosphorylserine, 473*t*
PHPA. *See* 1-Palmitoyl-*sn*-glycero-3-(dihydrogen phosphate) (PHPA)
PHPC. *See* 1-Palmitoyl-*sn*-glycero-3-phosphocholine (PHPC)
PHPE. *See* 1-Palmitoyl-*sn*-glycero-3-phospho-1′-ethanolamine (PHPE)
PHPG. *See* 1-Palmitoyl-*sn*-glycero-3-phospho-*sn*-1′-glycerol (PHPG)
PHPI. *See* 1-Palmitoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (PHPI)
PHPS. *See* 1-Palmitoyl-*sn*-glycero-3-phospho-L-serine (PHPS)
*Phragmites australis*, 312*t*
*Phragmites communis* (Water Reed), 18*t*, 33*t*, 223*t*
*Phyllitis scolopendrium* (Hart's Tongue Fern), 223*t*
*Phyllocactus* spp., 413*t*
*Phellodendron wilsonii*, 312*t*, 475–490
*Phylloglossum drummondii*, 89*t*
*Phyllospadix iwatensis*, 223*t*
*Phyllostachys bambusoides* (Timber Bamboo), 312*t*
*Phyllostachys nigra* (Black Bamboo), 312*t*
*Phyllostachys pubescens* (Moso Bamboo), 223*t*, 312*t*, 392*t*, 413*t*
*Physalis ixocarpa* (Tomatillo), 89*t*
*Physalis peruviana* (Cape Gooseberry), 89*t*
Phytic Acid ($InsP_6$), 1, 75–134, 135–136, 136*t*, 137–138, 137*t*, 141, 143*f*, 145*f*, 147, 147*f*, 149, 151, 152*t*, 162–163, 457–461, 471, 472*t*, 473*t*, 475–500
Phytin, 75, 79, 82, 86*t*, 87–88
Phytoglycolipid, 475–490
Pi. *See* Phosphoric Acid (Pi)
*Picea abies* (Norway Spruce), 18*t*, 42*t*, 178*t*, 189*t*, 223*t*, 312*t*, 413*t*, 446*t*, 475–500
*Picea glauca* (White Spruce), 89*t*
*Picea mariana* (Black Spruce), 89*t*, 223*t*, 462*t*, 490–500
*Picea pungens* (Colorado Spruce), 89*t*, 475–490
*Picea* spp. (Spruce), 89*t*
*Pimpinella anisum*, 223*t*
*Pinusmugo* (Mugo Pine)
  ssp. *mughus*, 89*t*
  ssp. *rostrata*, 89*t*
PIP. *See* Phosphatidylinositol Phosphate (PIP)
$PIP_2$. *See* Phosphatidylinositol Bisphosphate ($PIP_2$)
*Piper clusii* (African Cubeb), 89*t*
*Piper guineense* (Guinea Cubeb, Etinkane), 89*t*
*Piper nigrum* (Black Pepper), 89*t*
*Pisonia alba* (Lettuce Tree), 89*t*
*Pistacia atlantica* (Mt. Atlas Mastic Tree), 89*t*
*Pistacia mutica* (Mt. Atlas Mastic Tree), 312*t*
*Pistia stratiotes* (Water Lettuce), 223*t*
*Pisum sativum* (Pea), 6–7, 7*t*, 18*t*, 33*t*, 42*t*, 66*t*, 68*t*, 70*t*, 78*t*, 89*t*, 139*t*, 152*t*, 158*t*, 178*t*, 189*t*, 196*t*, 200*t*, 208*t*, 212*t*, 223*t*, 312*t*, 380*t*, 392*t*, 413*t*, 432*t*, 446*t*, 455*t*, 462*t*, 469*t*, 472*t*, 475–500
*Pithecellobium dulce* (Manila Tamarind, Korukapalli), 89*t*
*Pithecellobium flexicaule* (Ébano), 89*t*
PL. *See* Phospholipids (PL)
*Plagiomnium ellipticum*, 223*t*
*Plagiomnium medium*, 223*t*
Plane Tree. *See Platanus* spp.
*Plantago lanceolata* (Narrowleaf Plantain), 413*t*
Plantain. *See Musa* × *paradisiaca*
Plantain, Narroleaf. *See Plantago lanceolata*
Plantain, Water. *See Alisma orientale*

*Platanus occidentalis* (Eastern Sycamore), 312*t*, 446*t*
*Platanus* spp. (Plane Tree), 223*t*, 490–500
*Platycerium alcicorne*, 223*t*, 413*t*
*Pleurozium schreberi*, 223*t*
PLnPA. *See* 1-Palmitoyl-2-linolenoyl-*sn*-glycero-3-(dihydrogen phosphate) (PLnPA)
PLnPC. *See* 1-Palmitoyl-2-linolenoyl-*sn*-glycero-3-phosphocholine (PLnPC)
PLnPE. *See* 1-Palmitoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-ethanolamine (PLnPE)
PLnPG. *See* 1-Palmitoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (PLnPG)
PLnPI. *See* 1-Palmitoyl-2-linolenoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (PLnPI)
PLP. *See* Pyridoxal 5′-Phosphate (PLP)
PLPA. *See* 1-Palmitoyl-2-linoleoyl-*sn*-glycero-3-(dihydrogen phosphate) (PLPA)
PLPC. *See* 1-Palmitoyl-2-linoleoyl-*sn*-glycero-3-phosphocholine (PLPC)
PLPE. *See* 1-Palmitoyl-2-linoleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (PLPE)
PLPG. *See* 1-Palmitoyl-2-linoleoyl-*sn*-glycero-3-phospho-1′*sn*-glycerol (PLPG)
PLPI. *See* 1-Palmitoyl-2-linoleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (PLPI)
PLPS. *See* 1-Palmitoyl-2-linoleoyl-*sn*-glycero-3-phospho-L-serine (PLPS)
Plum. *See Prunus domestica*
PMP. *See* Pyridoxamine 5′-Phosphate (PMP)
PNP. *See* Pyridoxine 5′-Phosphate (PNP)
*Poa annua* (Annual Bluegrass), 81, 89*t*, 223*t*, 312*t*, 469*t*
*Poa pratensis* (Kentucky Bluegrass), 223*t*
Podocarp, Cloud. *See Podocarpus nubigenus*
*Podocarpus macrophyllus* (Yew Plum Pine), 312*t*, 475–490
*Podocarpus nivalis* (Snow Totara), 223*t*
*Podocarpus nubigenus* (Manio, Cloud Podo-carp), 223*t*
*Podocarpus salignus* (Willow Podocarp), 223*t*
Podocarp, Willow. *See Podocarpus salignus*
Poinciana, Royal. *See Delonix regia*
*Polygonum amphibium* (Water Smartweed), 223*t*
*Polypodium vulgare* (European Polypody), 223*t*
Polypody. *See Polypodium vulgare*
*Polystichum* spp., 7*t*
*Polytrichum commune* (Polytrichum Moss), 223*t*, 413*t*
*Polytrichum juniperinum* (Hair Cap Moss), 223*t*
Pomegranate. *See Punica granatum*
Pomelo. *See Citrus paradisi*
*Poncirus trifoliata* × *Citrus paradisi* (Citrumelo), 223*t*
Pondweed, Flatstem. *See Potamogeton zosteriformis*
Pondweed, Floating Leaf. *See Potamogeton natans*
Pondweed, Perfoliate. *See Potamogeton perfoliatus*
*Pongamia glabra* (Pongam, Karanja), 223*t*
POPA. *See* 1-Palmitoyl-2-oleoyl-*sn*-glycero-3-(dihydrogen phosphate) (POPA)
POPC. *See* 1-Palmitoyl-2-oleoyl-*sn*-glycero-3-phosphocholine (POPC)
POPE. *See* 1-Palmitoyl-2-oleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (POPE)
POPG. *See* 1-Palmitoyl-2-oleoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (POPG)
POPI. *See* 1-Palmitoyl-2-oleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (POPI)
Poplar, Black. *See Populus nigra*
Poplar, Carolina. *See Populus euramericana*
Poplar, Lombardy. *See Populus nigra*, var. *italica*
Poppy, California. *See Escholtzia californica*
Poppy, Corn. *See Papaver rhoeas*
Poppy, Field. *See Papaver dubium*
Poppy, Opium. *See Papaver somniferum*
Poppy, Oriental. *See Papaver orientale*
Poppy, Roemer. *See Roemeria refracta*
Poppy, Sea. *See Glaucium fimbrilligerum*
POPS. *See* 1-Palmitoyl-2-oleoyl-*sn*-glycero-3-phospho-L-serine (POPS)

*Populus deltoides* (Eastern Cottonwood), 18*t*, 42*t*, 392*t*
ssp. *caudina*, 413*t*
*Populus euroamericana* (Carolina Poplar), 223*t*
ssp. *gelrica*, 223*t*
*Populus nigra* (Black Poplar), 18*t*, 29*t*, 33*t*, 42*t*, 66*t*, 413*t*, 490–500
var. *italica* (Lombardy Poplar), 223*t*
*Populus tremula* (European Aspen), 42*t*, 413*t*
*Porphyra tenera* (Nori), 432*t*
*Portulaca grandiflora* (Rose Moss), 18*t*, 223*t*, 312*t*, 432*t*, 490–500
*Portulaca oleracea* (Purslane), 89*t*, 223*t*, 490–500
*Posidonia oceanica* (Mediterranean Tapeweed), 223*t*
*Potamogeton filiformis*, 223*t*
*Potamogeton natans* (Floating Leaf Pondweed), 223*t*
*Potamogeton perfoliatus* (Perfoliate Pondweed), 223*t*
*Potamogeton zosteriformis* (Flatstem Pondweed), 380*t*
Potato. *See Solanum tuberosum*
Potato, Air. *See Dioscorea bulbifera*
Potato, Sweet. *See Ipomoea batatas*
Potato, Telingo. *See Amorphophallus campanulatus*
Potato, Wild. *See Solanum acaule*; *Solanum schreiteri*
*Potentilla asiatica* (Cinquefoil), 89*t*, 223*t*
*Poterium polygamum*, 89*t*
P(3t)PG. *See* 1-Palmitoyl-2-*trans*-3-hexadecenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (P(3t)PG)
PPi. *See* Di-(or Pyro)phosphoric Acid (PPi)
*Premna odorata* (Premna), 89*t*
Prince's Feather. *See Amaranthus hypochondriacus*
*Pringlea antiscorbutica* (Kerguelen Cabbage), 223*t*
*Prosopis africana*, 89*t*
*Prosopis chilensis* (Algarrobo), 89*t*
*Prosopis glandulosa* (Honey Mesquite), 89*t*
*Prosopis velutina* (Velvet Mesquite), 88, 89*t*
*Protea compacta*, 89*t*
*Prunus armeniaca* (Apricot), 18*t*, 37, 42*t*, 63*t*, 89*t*, 413*t*, 446*t*, 490–500
*Prunus avium* (Sweet Cherry), 89*t*, 223*t*, 490–500
*Prunus bucharica*, 89*t*
*Prunus cerasus* (Morello Cherry), 223*t*, 413*t*
*Prunus domestica* (Plum), 89*t*, 223*t*
*Prunus dulcis* (Almond), 89*t*, 223*t*, 413*t*, 446*t*, 475–490
*Prunus laurocerasus* (Cherry Laurel), 89*t*
*Prunus mahaleb* (Mahaleb Cherry), 89*t*
*Prunus mume* (Japanese or Ume Apricot), 223*t*, 490–500
*Prunus padus* (Bird Cherry), 312*t*
*Prunus persica* (Peach), 89*t*, 223*t*, 312*t*, 413*t*, 475–500
ssp. *nectarina* (Nectarine), 312*t*
*Prunus petunnikowii*, 89*t*
*Prunus sargentii* (Sargent Cherry), 312*t*
PS. *See* Phosphatidylserine (PS)
*Pseudobryum cinclidioides*, 223*t*
*Pseudosasa japonica* (Arrow Bamboo), 446*t*
*Pseudotsuga menziesii* (Douglas Fir), 446*t*
*Psidium guajava* (Guava), 89*t*
*Psilotum triquetrum*, 223*t*
*Psophocarpus tetragonolobus* (Winged Bean), 89*t*, 223*t*, 475–490
*Psoralea drupacea* (Drupe Scurf Pea), 89*t*, 223*t*
*Pteridium aquilinum* (Bracken Fern), 223*t*, 312*t*, 392*t*
*Pterocarpus mildbraedii* (Mkpa), 89*t*
*Pterocarpus osun* (African Padauk), 89*t*
*Pueraria hirsuta* (Kudzu), 70*t*
Pummelo. *See Citrus grandis*
Pumpkin. *See Cucurbita pepo*
Pumpkin, Fluted. *See Telfairia occidentalis*
*Punica granatum* (Pomegranate), 89*t*, 223*t*
Purslane. *See Portulaca oleracea*
Purslane, Sea. *See Sesuvium portulacastrum*
Pyinkado, Burma. *See Xylia xylocarpa*
Pyridoxal 5′-Phosphate (PLP), 450–451, 452, 453, 454–455, 455*t*, 475–500
Pyridoxamine 5′-Phosphate (PMP), 450–451, 451*f*, 452, 453, 455*t*, 475–490

Pyridoxine 5′-Phosphate (PNP), 451, 450–451, 451*f*, 452, 453, 455, 455*t*
*Pyrus communis* (Pear), 18*t*, 33*t*, 42*t*, 66*t*, 223*t*, 312*t*, 413*t*, 446*t*, 490–500
*Pyrus pyrifolia* ssp. *culta* (Nashi), 223*t*
*Pyrus serotina* (Japanese Pear), 413*t*

**Q**

Quandong. *See Santalum acuminatum*
Queen Anne's Lace. *See Daucus carota*, ssp. *carota*
*Quercus borealis* (Red Oak), 34–35, 312*t*
*Quercus lusitanica* (Portuguese Oak), 89*t*
*Quercus mongolica* ssp..*grosseserrata*, 312*t*
*Quercus palustris* (Pin Oak), 223*t*
*Quercus petraea* (Durmast Oak), 312*t*
*Quercus phellos* (Willow Oak), 312*t*
*Quercus robur* (English Oak), 89*t*, 223*t*, 312*t*
*Quercus rubra* (Northern Red Oak), 18*t*, 33*t*, 42*t*
*Quercus* spp. (Oak), 89*t*
Quince. *See Cydonia oblonga*
Quince, Japanese. *See Chaenomeles japonica*
Quinoa. *See Chenopodium quinoa*

**R**

Radish. *See Raphanus sativus*
Radish, Japanese. *See Raphanus acanthiformis*
Ragi. *See Eleusine coracana*
Rain Tree. *See Samanea saman*
Rain Tree, Golden. *See Koelreuteria paniculata*
*Ramonda nathaliae*, 223*t*
*Ramonda serbica*, 223*t*
*Ranunculus glacialis* (Glacier Buttercup), 223*t*
*Ranunculus* spp. (Buttercup), 89*t*
Rape. *See Brassica napus*
Rape, Oilseed. *See Brassica oleracea*
Rape, Turnip. *See Brassica campestris*; *Brassica rapa*
Rape, White Turnip. *See Brassica rapa*, ssp. *rapa*
Rape, Winter. *See Brassica napus*, ssp. *oleifera*
*Raphanus acanthiformis* (Japanese Radish), 200*t*, 312*t*
*Raphanus sativus* (Radish), 18*t*, 33*t*, 42*t*, 70*t*, 89*t*, 178*t*, 189*t*, 200*t*, 223*t*, 312*t*, 380*t*, 413*t*, 432*t*, 446*t*, 475–500
ssp. *radicola* (Radish), 223*t*
*Raphia farinifera* (Raffia Palm), 223*t*
*Raphia hookeri* (Ivory Coast Raffia Palm), 223*t*
*Raphia regalis*, 223*t*
*Raphia sudanica*, 223*t*
*Raphia vinifera* (Wine Palm), 223*t*
Rattleweed. *See Crotalaria retusa*
Ratu. *See Cassia sieberiana*
*Rauvolfia serpentina* (Indian Snakeroot), 178*t*, 189*t*, 208*t*, 223*t*
*Rauvolfia vomitoria* (Swizzlestick), 89*t*
Redwood, Dawn. *See Metasequoia glyptostroboides*
*Reseda lutea* (Yellow Mignonette), 413*t*
RF. *See* Riboflavin
Rhamnose-1-Phosphate (Rha1P), 387–388
Rha1P. *See* Rhamnose-1-Phosphate (Rha1P)
*Rhaponticum integrifolium*, 89*t*, 223*t*
*Rhododendron ponticum* (Common Rhododendron), 18*t*, 42*t*
*Rhododendron* spp., 223*t*
*Rhodomyrtus tomentosa* (Downy Myrtle), 89*t*
*Rhus hirta* (Staghorn Sumac), 89*t*
*Ribes nigrum* (Black Currant), 223*t*
*Ribes sinanense*, 312*t*
Riboflavin (RF), 405, 429–438, 430*f*, 432*t*, 439
Ribonucleic acid (RNA), 305–306, 307–308, 312*t*, 349, 350, 460, 472, 473*t*
Ribose 5-Phosphate (R5P), 1, 4*t*, 6*t*, 10, 11, 14, 29–30, 30*f*, 31–32, 33*t*, 34–35, 63, 64–65, 354, 406–407, 490–500
Ribulose 1,5-Bisphosphate (Ru1,5P), 1, 4*t*, 6–7, 6*f*, 6*t*, 8–9, 9*f*, 10, 29–30, 30*f*, 31, 32, 33*t*, 34–35, 490–500
Ribulose 5-Phosphate (Ru5P), 1, 6*t*, 11, 29–30, 30*f*, 31, 32, 33*t*, 34–35, 36–37, 53, 430
*Riccia fluitans* (Crystalwort), 223*t*
Rice. *See Oryza sativa*
*Ricinus communis* (Castor Bean), 18*t*, 42*t*, 68*t*, 89*t*, 200*t*, 223*t*, 312*t*, 392*t*, 413*t*, 462*t*, 475–500
Rimas. *See Artocarpus altilis*
RNA. *See* Ribonucleic Acid

*Robinia pseudoacacia* (Black Locust), 66*t*, 223*t*, 312*t*, 380*t*, 413*t*, 432*t*, 490–500
Rocket Salad. *See Eruca sativa*
Rockrose. *See Cistus ladanifer*
*Roemeria refracta* (Roemer Poppy), 89*t*, 223*t*
Ronji. *See Vigna auriculata*
*Rorippa amphibia* (Amphibious Marsh Cress), 223*t*
*Rosa canina* (Dog Rose), 89*t*, 223*t*
*Rosa damascena* (Damask Rose), 312*t*, 412, 413*t*
*Rosa rubiginosa* (Sweetbrier Rose), 89*t*
*Rosa rugosa* (Turkestan Rose), 223*t*
Roselle. *See Hibiscus sabdariffa*
Rose Moss. *See Portulaca grandiflora*
Rowan. *See Sorbus aucuparia*
R5P. *See* Ribose 5-Phosphate (R5P)
Rubber Tree, Pará. *See Hevea brasiliensis*
*Rubia tinctorum* (Madder), 89*t*
*Rubus* spp. (Blackberry), 89*t*, 223*t*
Rue. *See Ruta graveolens*
Rue, African. *See Peganum harmala*
*Rumex acetosa* (Sorrel), 89*t*, 223*t*
*Rumex halaczii*, 89*t*
*Rumex vesicarius* (Chukai Shak), 89*t*
Ru1,5P. *See* Ribulose 1,5-Bisphosphate
Ru5P. *See* Ribulose 5-Phosphate
Rush, Needlegrass. *See Juncus roemerianus*
Rutabaga. *See Brassica napobrassica*
*Ruta graveolens* (Rue), 223*t*
Rye. *See Secale cereale*
Ryegrass, Italian. *See Lolium multiflorum*
Ryegrass, Perennial. *See* Lolium perenne
Ryegrass, Poison. *See Lolium cuneatum*

## S

*Saccharum officinarum* (Sugarcane), 4*t*, 18*t*, 42*t*, 223*t*, 312*t*, 392*t*, 413*t*, 469*t*
*Saccharum sinense*, 18*t*
*Saccharum* spp., 42*t*, 212*t*
Safflower. *See Carthamus tinctorius*
Safflower, Wild. *See Carthamus oxycantha*
Sagargota. *See Caesalpinia bonducella*
Sage. *See Salvia macrosiphon*
Sage, Shrubby Jerusalem. *See Phlomis fruticosa*
Sage, Yellow. *See Lantana camara*, ssp. *aculeata*
*Sagittaria sagittifolia* (Arrowhead), 223*t*, 446*t*
*Sagittaria trifolia* (Chinese Arrowhead), 70*t*
*Salicornia arabica*, 223*t*
*Salicornia europaea* (Samphire), 223*t*
*Salix alba* (White Willow), 312*t*, 413*t*
*Salix babylonica* (Weeping Willow), 312*t*
*Salix cinerea* (Large Gray Willow), 413*t*
*Salix daphnoides*, 312*t*
*Salix fragilis* (Crack Willow), 413*t*
*Salix herbacea* (Dwarf Willow), 223*t*
*Salix matsudana* ssp. *tortuosa* (Dragon-Claw Willow), 312*t*
*Salix nigricans* (Dark-Leaved Willow), 413*t*
*Salix reticulata* (Netleaf Willow), 223*t*
*Salix retusa* (Notchleaf Willow), 223*t*
*Salix triandra* (Almond Willow), 18*t*, 42*t*, 312*t*, 392*t*, 469*t*
*Salix viminalis* (Basket Willow), 312*t*, 413*t*
*Salsola gemmascens*, 462*t*, 490–500
*Salsola sclerantha*, 462*t*, 490–500
Saltgrass, Coastal. *See Distichlis spicata*
*Salvadora oleoides* (Khakan), 223*t*
Salvation Jane. *See Echium plantagineum*
*Salvia macrosiphon* (Sage), 89*t*
*Salvinia nutans*, 223*t*
*Samanea saman* (Rain Tree), 140, 143, 145, 152*t*, 212*t*
*Sambucus nigra* (European Elder), 223*t*, 432*t*
*Sambucus sieboldiana* ssp. *miquelii*, 312*t*
Samphire. *See Salicornia europaea*
*Sandoricum koetjape* (Santol), 89*t*
*Santalum acuminatum* (Quandong), 89*t*
Santol. *See Sandoricum koetjape*
*Sapium sebiferum* (Vegetable Tallow Tree), 223*t*
*Saponaria vaccaria* (Cow Cockle), 223*t*, 312*t*
*Saposhnikovium* spp., 89*t*
Sarson, Yellow. *See Brassica campestris*, ssp. *sarson*
*Sauromatum guttatum* (Voodoo Lily), 312*t*
*Saussuria depressa*, 223*t*
*Saxegothaea conspicua* (Prince Albert Yew), 223*t*
Scallion. *See Allium ascalonicum*

*Scilla hispanica* (Spanish Bluebell), 413*t*
*Scirpus holoschoemus* (Roundhead Bulrush), 413*t*
*Scirpus subterminalis*, 380*t*
Scouring Bush, Dwarf. *See Equisetum scirpoides*
Seablite. *See Suaeda maritima*
Seablite, Annual. *See Suaeda maritima*, var. *macrocarpa*
Sea Purse. *See Dioclea reflexa*
Seaweed, 432*t*, 455*t*
Seaweed, Brown. *See Laminaria japonica*
Seawrack. *See Zostera marina*
*Secale cereale* (Rye), 33*t*, 42*t*, 70*t*, 89*t*, 152*t*, 178*t*, 189*t*, 200*t*, 208*t*, 223*t*, 312*t*, 380*t*, 413*t*, 432*t*, 455*t*, 458*t*, 462*t*, 475–500
Sedoheptulose 1,7-Bisphosphate (Se1,7P), 1, 6*t*, 10, 28, 62, 63, 64–65, 66*t*
Sedoheptulose 7-Phosphate (Se7P), 1, 4*t*, 6*t*, 10, 11, 28, 29, 30, 54, 62, 63, 64–65, 66*t*, 473*t*, 490–500
Seepweed, Alkali. *See Suaeda fruticosa*
*Selaginella denticulata* (Toothleaved Clubmoss), 392*t*, 413*t*, 469*t*
*Selaginella kraussiana*, 223*t*
*Selaginella pallescens* (Moss Fern), 223*t*
*Selaginella selaginoides* (Club Spikemoss), 223*t*
*Selaginella uncinata* (Blue Spiemoss), 223*t*
*Selaginella willdenowii*, 223*t*
*Senecio cruentus* (Cineraria), 89*t*
*Senecio vulgaris* (Groundsel), 223*t*
Senna, Coffee. *See Cassia occidentalis*
Senna, Pig's. *See Cassia absus*
*Senna septentrionalis* (Arsenic Bush), 223*t*
Se1,7P. *See* Sedoheptulose 1,7-Bisphosphate (Se1,7P)
Se7P. *See* Sedoheptulose 7-Phosphate (Se7P)
*Sequoiadendron giganteum* (Giant Sequoia), 223*t*, 312*t*
Serendipity Berry. *See Dioscoreophyllum cumminsii*
*Sesamum alatum*, 18*t*, 42*t*
*Sesamum indicum* (Sesame), 42*t*, 89*t*, 223*t*, 413*t*, 462*t*, 475–500
*Sesbania grandiflora* (Scarlet Wistaria Tree, Agati), 89*t*
*Sesuvium portulacastrum* (Sea Purslane), 89*t*
*Setaria glauca* (Yellow Foxtail), 223*t*
*Setaria italica* (Italian or Foxtail Millet), 89*t*, 223*t*
*Setaria verticillata* (Bristly Foxtail), 223*t*, 413*t*
Shallot. *See Allium ascalonicum*
Shameplant. *See Mimosa pudica*
Shea Butter Tree. *See Butyrospermum paradoxum*
She Oak, Black. *See Casuarina littoralis*
She Oak, Slaty. *See Casuarina muelleriana*
Shepherd's Purse. *See Capsella bursapastoris*
Shield Fern. *See Dryopteris filix-mas*
SHPA. *See* 1-Stearoyl-*sn*-glycero-3-(dihydrogen phosphate) (SHPA)
SHPC. *See* 1-Stearoyl-*sn*-glycero-3-phosphocholine (SHPC)
SHPE. *See* 1-Stearoyl-*sn*-glycero-3-phospho-1′-ethanolamine (SHPE)
SHPG. *See* 1-Stearoyl-*sn*-glycero-3-phospho-*sn*-glycerol (SHPG)
SHPS. *See* 1-Stearoyl-*sn*-glycero-3-phospho-L-serine (SHPS)
Sicklepod. *See Cassia tora*
*Sicyos angulatus* (Bur Cucumber), 223*t*
*Simmondsia chinensis* (Jojoba), 89*t*, 223*t*
*Sinapis alba* (White Mustard), 89*t*, 312*t*, 380*t*, 392*t*, 413*t*, 469*t*, 475–490
Sisal. *See Agave sisalana*
Siseles. *See Alternanthera sessilis*
*Sison amomum* (Stone Parsley), 223*t*
SLnPC. *See* 1-Stearoyl-2-linolenoyl-*sn*-glycero-3-phosphocholine (SLnPC)
SLnPE. *See* 1-Stearoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-ethanolamine (SLnPE)
SLnPG. *See* 1-Stearoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (SLnPG)
SLnPI. *See* 1-Stearoyl-2-linolenoyl-*sn*-glycero-3-phospho-D-*myo*-Inositol (SLnPI)
SLPA. *See* 1-Stearoyl-2-linoleoyl-*sn*-glycero-3-(dihydrogen phosphate) (SLPA)
SLPC. *See* 1-Stearoyl-2-linoleoyl-*sn*-glycero-3-phosphocholine (SLPC)

SLPE. *See* 1-Stearoyl-2-linoleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (SLPE)
SLPG. *See* 1-Stearoyl-2-linoleoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (SLPG)
SLPI. *See* 1-Stearoyl-2-linoleoyl-*sn*-glycero-3-phospho-D-*myo*-Inositol (SLPI)
SLPS. *See* 1-Stearoyl-2-linoleoyl-*sn*-glycero-3-phospho-L-serine (SLPS)
Smartweed, Water. *See Polygonum amphibium*
*Smilax* spp. (Greenbrier), 223*t*
Snakeroot, Indian. *See Rauvolfia serpentina*
Snapdragon. *See Antirrhinum majus*
SODPG. *See* 1′,3′-bis(1-Stearoyl-2-oleoyl-*sn*-glycero-3-phospho)-1′-*sn*-glycerol (SODPG)
*Solanum acaule* (Wild Potato), 223*t*, 490–500
  ssp. *depexum*, 223*t*
  ssp. *punae*, 223*t*, 490–500
  ssp. *schreiteri*, 223*t*, 490–500
*Solanum africanum*, 89*t*
*Solanum argentinum*, 223*t*
*Solanum commersonii* (Commerson's Nightshade), 223*t*
*Solanum demissum* (Nightshade), 223*t*, 490–500
*Solanum gnomalum*, 89*t*
*Solanum maglia*, 223*t*, 490–500
*Solanum mauritianum* (Earleaf Nightshade), 89*t*
*Solanum melongena* (Eggplant, Brinjal), 89*t*, 212*t*, 223*t*, 312*t*
*Solanum nigrum* (Black Nightshade), 89*t*
*Solanum pamitanae*, 223*t*, 490–500
*Solanum phureja* (Nightshade), 70*t*
*Solanum rybinii*, 223*t*, 490–500
*Solanum sanctaerosae*, 223*t*, 490–500
*Solanum schreiteri* (Wild Potato), 223*t*
*Solanum tuberosum* (Potato), 2, 4–5, 18*t*, 33*t*, 451, 39, 41, 42*t*, 54, 58, 63*t*, 69, 70*t*, 81, 89*t*, 178*t*, 189*t*, 208*t*, 223*t*, 311, 312*t*, 380*t*, 392*t*, 406, 412, 413*t*, 429, 432*t*, 446*t*, 455*t*, 458*t*, 462*t*, 469*t*, 471, 472*t*, 475–500
*Sonneratia alba*, 380*t*
So1P. *See* Sorbitol 1-Phosphate (So1P)
So6P. *See* Sorbitol 6-Phosphate (So6P)
SOPA. *See* 1-Stearoyl-2-oleoyl-*sn*-glycero-3-(dihydrogen phosphate) (SOPA)
SOPC. *See* 1-Stearoyl-2-oleoyl-*sn*-glycero-3-phosphocholine (SOPC)
SOPE. *See* 1-Stearoyl-2-oleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (SOPE)
SOPG. *See* 1-Stearoyl-2-oleoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (SOPG)
*Sophora japonica* (Japanese Pagoda Tree), 89*t*, 223*t*, 475–490
SOPI. *See* 1-Stearoyl-2-oleoyl-*sn*-glycero-3-phospho-D-*myo*-Inositol (SOPI)
SOPS. *See* 1-Stearoyl-2-oleoyl-*sn*-glycero-3-phospho-L-serine (SOPS)
Sorbitol 1-Phosphate (So1P), 1, 35, 36, 37, 38, 39, 41
Sorbitol 6-Phosphate (So6P), 1, 35, 36, 37, 39, 40, 41
*Sorbus aucuparia* (Rowan), 5, 223*t*, 346
*Sorbus commixta* (Mountain Ash), 312*t*
*Sorghum bicolor* (Sorghum), 7*t*, 18*t*, 42*t*, 70*t*, 89*t*, 152*t*, 223*t*, 310–311, 312*t*, 392*t*, 413*t*, 462*t*, 472*t*, 475–500
  var. *cernuum* (White Durra), 223*t*
*Sorghum halepense* (Johnson Grass), 89*t*
*Sorghum sudanense*, 312*t*
Sorrel. *See Rumex acetosa*
Soursop. *See Annona muricata*
Soybean. *See Glycine max*; *Glycine soja*
*Spartina alterniflora* (Smooth Cordgrass), 18*t*, 312*t*, 490–500
*Spartina cynosuroides*, 490–500
*Spartina patens* (Saltmeadow Cordgrass), 223*t*, 312*t*, 490–500
Spatterdock. *See Nuphar advena*
Spearmint. *See Mentha spicata*
Spelt. *See Triticum spelta*
S(3t)PG. *See* 1-Stearoyl-2-*trans*-3-hexadecenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (S(3t)PG)
*Sphagnum nemorium*, 223*t*
*Sphagnum palustre* (Prairie Sphagnum), 223*t*
*Sphagnum squarrosum* (Sphagnum), 223*t*
*Sphenostylis stenocarpa* (African Yambean), 89*t*

Spiderlily, Red. *See Lycoris radiata*
Spider Plant. *See Chlorophytum comosum*
Spikemoss, Blue. *See Selaginella uncinata*
Spikemoss, Club. *See Selaginella selaginoides*
Spinach. *See Spinacia oleracea*
Spinach, New Zealand. *See Tetragonia expansa*
Spinach, Philippine. *See Talinum triangulare*
*Spinacia oleracea* (Spinach), 7*t*, 18*t*, 33*t*, 42*t*, 65, 66*t*, 68*t*, 89*t*, 161*t*, 178*t*, 223*t*, 312*t*, 392*t*, 413*t*, 432*t*, 446*t*, 469*t*, 472*t*
*Spinacia turkestanica*, 89*t*
Spindle Tree, European. *See Euonymus europaeus*
Spindle Tree, Japanese. *See Euonymus japonica*
*Spirodela oligorrhiza* (Duckweed), 18*t*, 42*t*, 59, 63*t*, 68*t*, 223*t*, 380*t*, 392*t*, 457, 462*t*, 469*t*, 472, 473*t*
*Spirodela polyrrhiza* (Giant Duckweed), 89*t*, 140, 143, 145, 148, 150, 152*t*, 156, 158*t*, 212*t*, 215, 223*t*, 413*t*
Spleenwort, Green. *See Asplenium viride*
*Spondias mombin* (Yellow Mombin), 89*t*
*Spondias purpurea* (Red Mombin), 89*t*
SPPG. *See* 1-Stearoyl-2-palmitoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (SPPG)
Spruce. *See Picea* spp.
Spruce, Black. *See Picea mariana*
Spruce, Colorado. *See Picea pungens*
Spruce, Norway. *See Picea abies*
Spruce, White. *See Picea glauca*
Spurge, Caper. *See Euphorbia lathyris*
Squash. *See Cucurbita digitata*; *Cucurbita palmata*
Squash, Hubbard. *See Cucurbita maxima*
Squash, Warty. *See Cucurbita moschata*
Squash, Winter. *See Cucurbita andreana*
Squash, Zucchini. *See Cucurbita pepo*, ssp. *melopepo*
*Stachys officinalis* (Common Hedgenettle), 413*t*
Starapple, African. *See Chrysophyllum albidum*
Starch phosphate, 68–69
1-Stearoyl-2-linolenoyl-*sn*-glycero-3-phosphocholine (SLnPC), 175, 177
1-Stearoyl-2-linolenoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (SLnPI), 211
1-Stearoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-ethanolamine (SLnPE), 187, 192
1-Stearoyl-2-linolenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (SLnPG), 200*t*
1-Stearoyl-2-linoleoyl-*sn*-glycero-3-(dihydrogen phosphate) (SLPA), 221
1-Stearoyl-2-linoleoyl-*sn*-glycero-3-phosphocholine (SLPC), 175, 177
1-Stearoyl-2-linoleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (SLPI), 210
1-Stearoyl-2-linoleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (SLPE), 187, 192
1-Stearoyl-2-linoleoyl-*sn*-glycero-3-phospho-L-serine (SLPS), 218
1-Stearoyl-2-linoleoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (SLPG), 200*t*
1-Stearoyl-2-oleoyl-*sn*-glycero-3-(dihydrogen phosphate) (SOPA), 207, 221
1-Stearoyl-2-oleoyl-*sn*-glycero-3-phosphocholine (SOPC), 175, 177
1-Stearoyl-2-oleoyl-*sn*-glycero-3-phospho-D-*myo*-inositol (SOPI), 210, 211–212
1-Stearoyl-2-oleoyl-*sn*-glycero-3-phospho-1′-ethanolamine (SOPE), 187, 192
1-Stearoyl-2-oleoyl-*sn*-glycero-3-phospho-L-serine (SOPS), 217, 218
1-Stearoyl-2-oleoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (SOPG), 200*t*
1-Stearoyl-2-palmitoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (SPPG), 199
1-Stearoyl-*sn*-glycero-3-(dihydrogen phosphate) (SHPA), 185, 222
2-Stearoyl-*sn*-glycero-3-(dihydrogen phosphate) (HSPA), 222
1-Stearoyl-*sn*-glycero-3-phosphocholine (SHPC), 177, 183, 184, 185, 222
1-Stearoyl-*sn*-glycero-3-phospho-1′-ethanolamine (SHPE), 193, 194
1-Stearoyl-*sn*-glycero-3-phospho-L-serine (SHPS), 219
1-Stearoyl-*sn*-glycero-3-phospho-*sn*-glycerol (SHPG), 205, 206

1-Stearoyl-2-*trans*-3-hexadecenoyl-*sn*-glycero-3-phospho-1′-*sn*-glycerol (S(3t)PG), 199
*Stellaria media* (Chickweed), 413*t*, 432*t*
*Sterculia foetida* (Indian Almond, Jangli Badam), 89*t*, 223*t*
*Stillingia* spp. (Toothleaf), 89*t*
*Stizolobium aterrimum* (Bengal Bean), 89*t*
Strawberry. *See Fragaria* spp.
Strawberry Tree. *See Arbutus unedo*
Strawberry, Woodland. *See Fragaria vesca*
*Strelitzia reginae* (Bird of Paradise), 89*t*
*Striga asiatica* (Witchweed), 223*t*, 475–490
*Striga aspera*, 223*t*
*Striga hermonthica* (Purple Witchweed), 223*t*
*Strophanthus hispidus*, 413*t*
*Stylidium petiolare*, 89*t*
*Suaeda fruticosa* (Alkali Seepweed), 223*t*
*Suaeda maritima* (Seablite) var. *macrocarpa* (Annual Seablite), 223*t*
*Suaeda maritima* (Seablite), 223*t*
Sucrose 6′-Phosphate, 67–68, 68*t*
Sudachi. *See Citrus sudachi*
Sugarcane. *See Saccharum officinarum*
Sugar nucleotides, 305, 387–404, 388*f*, 392*t*
Sugar phosphates, 1–73, 80, 86, 308–309, 468, 471, 473*t*
Sultana. *See Impatiens sultanii*
Sultan, Sweer. *See Centaurea moschata*
Sumac, Chinese. *See Ailanthus glandulosa*
Sumac, Staghorn. *See Rhus hirta*
Sunflower. *See Helianthus annuus*
Sunnhemp. *See Crotalaria juncea*
Sweetsop. *See Annona squamosa*
*Swietenia mahogani* (West Indian Maho-gany), 223*t*
Swizzlestick. *See Rauvolfia vomitoria*
Sycamore, Eastern. *See Platanus occidentalis*

**T**

*Talinum triangulare* (Philippine Spinach, Fameflower), 89*t*
Tallow Tree, Vegetable. *See Sapium sebiferum*
Tamarack. *See Larix laricina*
Tamarind. *See Tamarindus indica*
Tamarind, Manila. *See Pithecellobium dulce*
*Tamarindus indica* (Tamarind, Tsamiya), 89*t*, 223*t*
Tampala. *See Amaranthus tricolor*
Tangelo. *See Citrus paradisi* x *Citrus reticulata*
Tangerine. *See Citrus reticulata*
Tangor. *See Citrus nobilis*
Tannia. *See Xanthosoma sagittifolium*
Tapeweed, Mediterranean. *See Posidonia oceanica*
*Tapinanthus dodoneifolius* (African Mistle-toe), 223*t*
Taramira. *See Eruca sativa*
Tara Vine. *See Actinidia arguta*
*Taraxacum* spp. (Dandelion), 200*t*
Taro. *See Colocasia esculenta*
Taro, Asian. *See Alocasia odora*
Taro, Egyptian. *See Colocasia antiquorum*
Taro, Giant. *See Alocasia macrorrhiza*
Tarwi. *See Lupinus mutabilis*
Tasselflower, Red. *See Emilia sonchifolia*
*Taxus baccata* (English Yew), 223*t*
*Taxus cuspidata* (Japanese Yew), 223*t*
TDP. *See* Thiamine Diphosphate (TDP); Thymidine 5′-Diphosphate (TDP)
TDPGalA. *See* Thymidine 5′-Diphosphate Galacturonic Acid (TDPGalA)
TDPGlc. *See* Thymidine 5′-Diphosphate Glucose (TDPGlc)
Tea. *See Camellia sinensis*; *Thea sinensis*
Tea, Assam. *See Camellia sinensis*, ssp. *assamica*
Teasel. *See Dipsacus fullonum*, var. *sylvestris*
*Telfairia occidentalis* (Fluted Pumpkin), 89*t*
Tenweeks Stock. *See Matthiola incana*
*Terminalia catappa* (Indian Almond), 89*t*
*Tetracarpidium conophorum* (Conophor), 89*t*
*Tetragonia expansa* (New Zealand Spinach), 223*t*
*Tetrapleura tetraptera*, 89*t*
*Tetrastigma harmandii* (Ayo), 89*t*
Tetrose Phosphates, 28–29, 28*f*, 29*t*
*Thalassia testudinum* (Turtle Grass), 312*t*
*Thea sinensis* (Tea), 413*t*
*Theobroma cacao* (Cocoa), 89*t*, 152*t*, 223*t*

*Thevetia neriifolia* (Yellow Oleander, Pivala Kanher), 223*t*
Thiamine Diphosphate (TDP), 440
Thiamine Monophosphate (TMP), 439, 440
Thiamine Triphosphate (TTP), 439, 441
Thistle, Black. *See Carduus acanthoides*
Thistle, Curly Plumeless. *See Carduus crispus*
Thistle, Scotch. *See Onopordon acanthium*
Thistle, Star. *See Centaurea calcitrapa*
Thistle, Yellow Star. *See Centaurea solstitialis*
Thorn Apple. *See Datura* spp.
Thorn Apple, Downy. *See Datura inoxia*
Thorn, Box. *See Lycium chinense*
*Thuidium tamariscinum* (Tamarisk Thu-idium Moss), 223*t*
Thymidine 5′-Diphosphate (TDP), 371
Thymidine 5′-Diphosphate Galacturonic Acid (TDPGalA), 392*t*
Thymidine 5′-Diphosphate Glucose (TDPGlc), 387–388, 392*t*
Thymidine 5′-Phosphate (TMP), 370
Thymidine 5′-Triphosphate (TTP), 371
5′-Thymidylic acid. *See* Thymidine 5′-Phosphate (TMP)
*Tilia platyphyllos* (Large-Leaved Linden), 18*t*, 42*t*, 312*t*, 392*t*
*Tillandsia usneoides*, 392*t*, 413*t*, 469*t*
TMP. *See* Thiamine Monophosphate (TMP); Thymidine 5′-Phosphate (TMP)
Tobacco. *See Nicotiana tabacum*
Tobacco, Aztec. *See Nicotiana rustica*
Tobacco, Jasmine. *See Nicotiana alata*
Tobacco, Longflower. *See Nicotiana longiflora*
Tobacco, Woodland. *See Nicotiana sylvestris*
Tomatillo. *See Physalis ixocarpa*
Tomato. *See Lycopersicon esculentum*
Tomato, Cherry. *See Lycopersicon esculentum*, ssp. *cerasiforme*
Tomato, Tree. *See Cyphomandra betacea*
Tomato, Wild. *See Lycopersicon hirsutum*, ssp. *glabratum*
Tonguefern, Hart's. *See Phyllitis scolopendrium*
Toothleaf. *See Stillingia* spp
Torch Tree. *See Ixora parviflora*
*Torreya nucifera* (Kaya Nut), 223*t*
*Tortula ruralis*, 312*t*
Tosa-Buntan. *See Citrus grandis*
Totara, Snow. *See Podocarpus nivalis*
TPN. *See* Nicotine Adenine Dinucleotide Phosphate
*Trapa natans* (Water Chestnut), 70*t*
*Treculia africana* (African Breadfruit), 89*t*
Trefoil, Birdsfoot. *See Lotus corniculatus*
*Trichodesma incanum*, 89*t*, 223*t*
*Trichopilia tortilis*, 223*t*
*Trichosanthes anguina* (Snake Gourd), 89*t*
*Trifolium alexandrinum* (Berseem Clover), 223*t*
*Trifolium incarnatum* (Crimson Clover), 312*t*, 475–490
*Trifolium pratense* (Red Clover), 42*t*, 89*t*, 200*t*, 223*t*, 413*t*, 458*t*, 490–500
*Trifolium repens* (White Clover, Ladino), 42*t*, 89*t*, 158*t*, 223*t*, 380*t*, 432*t*
*Trifolium* spp. (Hartshorn Clover), 89*t*, 223*t*
*Trifolium subterraneum* (Sub Clover), 18*t*, 42*t*, 89*t*, 392*t*, 475–490
*Trigonella corniculata*, 223*t*
*Trigonella foenum-graecum* (Fenugreek), 89*t*, 223*t*, 312*t*, 392*t*, 413*t*, 475–490
*Triose Phosphates*, 9–28, 9*f*, 18*t*, 58
*Triticosecale Witt.* (Triticale), 42*t*, 70*t*, 89*t*, 312*t*, 392*t*, 475–490
*Triticum aegilopoides* (Wild Einkorn), 223*t*
*Triticum aestivum* (Wheat), 18*t*, 33*t*, 42*t*, 66*t*, 70*t*, 78*t*, 89*t*, 139*t*, 152*t*, 158*t*, 161*t*, 178*t*, 189*t*, 196*t*, 200*t*, 223*t*, 312*t*, 380*t*, 392*t*, 413*t*, 432*t*, 446*t*, 455*t*, 458*t*, 462*t*, 469*t*, 475–500
*Triticum boeoticum* (Wild Einkorn), 413*t*
*Triticum compactum* (Club Wheat), 89*t*, 223*t*, 312*t*, 392*t*, 413*t*
*Triticum dicoccoides* (Wild Emmer), 223*t*, 413*t*
*Triticum dicoccum* (Emmer), 223*t*, 413*t*
*Triticum durum* (Durum Wheat), 33*t*, 89*t*, 223*t*, 312*t*, 413*t*, 458*t*, 462*t*, 475–490
*Triticum macha* (Macha Wheat), 223*t*
*Triticum monococcum* (Einkorn), 89*t*, 223*t*, 413*t*
*Triticum spelta* (Spelt), 89*t*, 223*t*, 413*t*, 475–490

*Triticum turgidum* (Poulard Wheat), 89*t*
Tsamiya. *See Tamarindus indica*
*Tsuga heterophylla* (Western Hemlock), 312*t*
TTP. *See* Thiamine Triphosphate (TTP); Thymidine 5′-Triphosphate (TTP)
*Tulipa* spp. (Tulip), 223*t*
Tulip Tree. *See Liriodendron tulipifera*
Tung, Chinese. *See Aleuritis montana*
Turmeric. *See Curcuma longa*
Turnip, White. *See Brassica rapa*, ssp. *rapa*
*Tussilago farfara* (Coltsfoot), 223*t*
*Typha latifolia* (Common Cattail), 223*t*

**U**

UDP. *See* Uridine 5′-Diphosphate (UDP)
UDPApi. *See* Uridine 5′-Diphosphate Apiose (UDPApi)
UDPAra. *See* Uridine 5′-Diphosphate Arabinose (UDPAra)
UDPFru. *See* Uridine 5′-Diphosphate Fructose (UDPFru)
UDPFuc. *See* Uridine 5′-Diphosphate Fucose (UDPFuc)
UDPG. *See* Uridine 5′-Diphosphate Glucose (UDPG/ UDPGlc)
UDPGal. *See* Uridine 5′-Diphosphate Galactose (UDPGal)
UDPGalA. *See* Uridine 5′-Diphosphate Galacturonic Acid (UDPGalA)
UDPGalNAc. *See* Uridine 5′-Diphosphate N-Acetylgalactosamine (UDPGalNAc)
UDPGlcA. *See* Uridine 5′-Diphosphate Glucuronic Acid (UDPGlcA)
UDPGlcNAc. *See* Uridine 5′-Diphosphate N-Acetylglucosamine (UDPGlcNAc)
UDPMan. *See* Uridine 5′-Diphosphate Mannose (UDPMan)
UDPRha. *See* Uridine 5′-Diphosphate Rhamnose (UDPRha)
UDPRib. *See* Uridine 5′-Diphosphate Ribose (UDPRib)
UDPX. *See* Uridine 5′-Diphosphate Sugars (UDPX)
UDPXyl. *See* Uridine 5′-Diphosphate Xylose (UDPXyl)
Ukpo. *See Mucuna sloanei*
*Ulmus davidiana* ssp. *japonica* (Japanese Elm), 312*t*
*Ulmus glabra* (Wych Elm), 312*t*
UMP. *See* Uridine 5′-Phosphate (UMP)
*Undaria pinnatifida* (Wakame), 432*t*
*Uniola paniculata* (Sea Oats), 475–490
Uridine 5′-Diphosphate (UDP), 59*f*, 305–307, 309*t*, 311–346, 312*t*, 347, 349, 360, 361, 362–363, 387–388, 389, 390, 391, 392*t*, 404, 413*t*, 473*t*, 475–500
Uridine 5′-Diphosphate Apiose (UDPApi), 392*t*
Uridine 5′-Diphosphate Arabinose (UDPAra), 389, 392*t*
Uridine 5′-Diphosphate Digitoxose (UDPDig), 392*t*
Uridine 5′-Diphosphate Fructose (UDPFru), 392*t*, 475–490
Uridine 5′-Diphosphate Fucose (UDPFuc), 392*t*
Uridine 5′-Diphosphate Galactose (UDPGal), 59, 311–346, 388*f*, 389, 390, 392*t*, 403, 475–500
Uridine 5′-Diphosphate Galacturonic Acid (UDPGalA), 388*f*, 390, 392*t*
Uridine 5′-Diphosphate Glucose (UDPG/ UDPGlc), 36*f*, 41–53, 59, 67, 309*t*, 311–346, 312*t*, 347, 349, 390, 391, 403, 404, 412, 471, 472*t*, 473*t*, 475–500
Uridine 5′-Diphosphate Glucuronic Acid (UDPGlcA), 388*f*, 389, 390, 392*t*
Uridine 5′-Diphosphate Mannose (UDPMan), 392*t*, 403
Uridine 5′-Diphosphate N-Acetylgalactosamine (UDPGalNAc), 389, 392*t*
Uridine 5′-Diphosphate N-Acetylglucosamine (UDPGlcNAc), 388*f*, 389, 390, 392*t*, 403, 475–500
Uridine 5′-Diphosphate Rhamnose (UDPRha), 392*t*
Uridine 5′-Diphosphate Ribose (UDPRib), 392*t*
Uridine 5′-Diphosphate Sugars (UDPX), 312*t*, 390, 392*t*, 403, 473*t*, 475–500

Uridine 5′-Diphosphate Xylose (UDPXyl), 388*f*, 389, 392*t*
Uridine 5′-Phosphate (UMP), 305–307, 309*t*, 311–346, 312*t*, 347, 349, 360, 361–363, 378, 391, 404, 413*t*, 473*t*, 475–500
Uridine 5′-Triphosphate (UTP), 59, 305–307, 309*t*, 311–346, 312*t*, 347, 349, 354, 360, 361, 362–363, 367, 372, 388*f*, 391, 403, 404, 472*t*, 473*t*, 475–500
5′-Uridylic acid. *See* Uridine 5′-Phosphate
*Urtica dioica* (Stinging Nettle), 42*t*, 223*t*
Utasi. *See Marsdenia latifolium*
UTP. *See* Uridine 5′-Triphosphate (UTP)
*Utricularia vulgaris* (Bladderwort), 223*t*

**V**

*Vaccaria segetalis* (Cow Herb), 89*t*
*Vaccinium macrocarpon* (Cranberry), 223*t*
*Vaccinium myrtillus* (Whortleberry), 223*t*
*Vallisneria gigantea* (Eelgrass), 223*t*
*Vallisneria spiralis*, 223*t*
*Vallisneria* spp. (Eelgrass), 223*t*
*Vanda teres*, 223*t*
Varagu. *See Paspalum scrobiculatum*
Vegetable Fern. *See Athyrium esculentum*
Velvetleaf. *See Abutilon theophrasti*
Velvetplant, Hawksbead. *See Crassocephalum crepidioides*
*Verbascum thapsus* (Mullein), 413*t*
*Vernonia amygdalina* (Bitter Leaf), 89*t*
*Vernonia galamensis* (Ironweed), 89*t*
Vetch. *See Vicia* spp.
Vetch, Hairy. *See Vicia villosa*
Vetch, Spring. *See Vicia sativa*
*Vicia faba* (Broad, Faba, Horse or Winds or Bean), 18*t*, 33*t*, 42*t*, 64–65, 66*t*, 70*t*, 89*t*, 152*t*, 178*t*, 189*t*, 196*t*, 200*t*, 208*t*, 223*t*, 312*t*, 363*t*, 380*t*, 392*t*, 413*t*, 432*t*, 462*t*, 469*t*, 475–500
  ssp. minor (Small Horse Bean), 89*t*, 152*t*, 475–490
*Vicia faba* ssp. *minor*, 89*t*, 152*t*, 223*t*
*Vicia sativa* (Spring Vetch), 312*t*, 413*t*
*Vicia* spp. (Vetch), 70*t*
*Vicia villosa* (Hairy Vetch), 223*t*
*Vigna aconitifolia* (Moth Bean), 89*t*, 475–490
*Vigna ambecensis*, 89*t*
*Vigna angularis* (Adzuki Bean), 89*t*, 178*t*, 189*t*, 196*t*, 200*t*, 208*t*, 223*t*, 312*t*, 413*t*, 432*t*, 475–490
*Vigna auriculata* (Ronji), 223*t*
*Vigna catjang* (Catjang), 89*t*
*Vigna luteola* (Hairypod Cowpea), 89*t*
*Vigna mungo* (Black Gram), 18*t*, 29*t*, 33*t*, 34–35, 42*t*, 66*t*, 89*t*, 161*t*, 223*t*, 312*t*, 380*t*, 392*t*, 432*t*, 475–500
*Vigna oblongifolia*, 89*t*
*Vigna racemosa*, 89*t*
*Vigna radiata* (Mung Bean, Green Gram), 18*t*, 42*t*, 70*t*, 89*t*, 152*t*, 223*t*, 312*t*, 392*t*, 413*t*, 432*t*, 462*t*, 475–490
*Vigna reticulata*, 89*t*
*Vigna sesquipedalis* (Yard-Long Bean), 89*t*, 413*t*, 475–490
*Vigna subterranea* (Bambara Groundnut), 89*t*
*Vigna umbellata* (Rice Bean), 89*t*, 475–490
*Vigna unguiculata* (Cowpea), 89*t*, 152*t*, 178*t*, 200*t*, 223*t*, 413*t*, 432*t*, 462*t*, 475–500
  ssp. *dekindtiana*, 89*t*
*Vigna vexillata* (Zombi Pea), 89*t*
  ssp. macrosperma, 223*t*
*Vinca erecta* (Periwinkle), 89*t*
*Vinca minor* (Periwinkle), 223*t*, 490–500
*Viola tricolor* (Field Pansy), 312*t*
Violet, Flame. *See Episcia reptans*
*Viscum album* (Mistletoe), 89*t*, 223*t*
*Vitamins*, 439–456
*Vitex doniana*, 89*t*
*Vitis coignetiae* (Crimson Glory Vine), 446*t*
*Vitis riparia* (Riverbank Grape), 223*t*
*Vitis* spp. (Grape), 432*t*
*Vitis vinifera* (Wine Grape), 18*t*, 42*t*, 89*t*, 223*t*, 312*t*, 490–500
*Voandzeia poissonii* (Dougoufoulo), 89*t*

**W**

Wakame. *See Undaria pinnatifida*
Wallflower, Gray. *See Erysimum diffusum*
Walnut, Black. *See Juglans nigra*
Walnut, English. *See Juglans regia*

*Washingtonia filifera* (California Fan Palm), 89*t*
Watercress. *See Nasturtium officinale*
Water Fern. *See Azolla africana*
Water Fern, Ray. *See Blechnum fluviatile*
Water Lily, Yellow. *See Nuphar luteum*
Water Meal. *See Wolffiella floridana*
Water Meal, Spotless. *See Wolffia arrhiza*
Watermelon. *See Citrullus lanatus*; *Citrullus vulgaris*
Water Moss. *See Fontinalis antipyretica*
Water Nymph. *See Najas flexilis*
Water Reed. *See Phragmites communis*
Water Sprite. *See Ceratopteris thalictroides*
Waterweed, Brazilian. *See Egeria densa*
Waterweed, Canadian. *See Elodea canadensis*
Waterweed, Western. *See Elodea nuttallii*
Wattle, Crowded-Leaf. *See Acacia conferta*
Wattle, Green. *See Acacia decurrens*
Wheat. *See Triticum aestivum*
Wheat, Club. *See Triticum compactum*
Wheat, Durum. *See Triticum durum*
Wheatgrass, Crested. *See Agropyron desertorum*
Wheat, Macha. *See Triticum macha*
Wheat, Poulard. *See Triticum turgidum*
Whortleberry. *See Vaccinium myrtillus*
Wild Bishop. *See Bifora radians*
Willow, Almond. *See Salix triandra*
Willow, Basket. *See Salix viminalis*
Willow, Crack. *See Salix fragilis*
Willow, Dark-Leaved. *See Salix nigricans*
Willow, Dragon-Claw. *See Salix matsudana*
Willow, Dwarf. *See Salix herbacea*
Willow, Large Gray. *See Salix cinerea*
Willow, Netleaf. *See Salix reticulata*
Willow, Notchleaf. *See Salix retusa*
Willow, Weeping. *See Salix babylonica*
Willow, White. *See Salix alba*
Wistaria Tree, Scarlet. *See Sesbania grandiflora*
Witchweed. *See Striga asiatica*
Witchweed, Purple. *See Striga hermonthica*
*Withania somnifera* (Winter Cherry, Aswa-gandh), 223*t*
*Wolffia arrhiza* (Spotless Water Meal), 312*t*, 413*t*
*Wolffiella floridana* (Water Meal), 89*t*, 490–500
Wormwood. *See Artemisia turanica*

**X**

*Xanthium orientale* (Oriental Cocklebur), 223*t*
*Xanthium pennsylvanicum* (Cocklebur), 312*t*, 475–490
*Xanthium strumarium* (Cocklebur), 18*t*, 33*t*, 42*t*, 223*t*, 446*t*
*Xanthosoma mafaffa* (Lime Zinger), 89*t*
*Xanthosoma sagittifolium* (Tannia), 89*t*
*Xanthosoma* spp. (Cocoyam), 89*t*
*Xylia xylocarpa* (Burma Pyinkado), 89*t*
*Xylomelum angustifolium*, 89*t*
*Xylopia aethiopica* (Guinea Pepper), 89*t*
Xylose 1-Phosphate (Xyl1P), 388*f*
Xylulose 5-Phosphate (Xu5P), 1, 6*t*, 10, 11, 28, 29–30, 31, 32, 33*t*, 34–35, 53, 54, 63, 64, 65

**Y**

Yam. *See Dioscorea versicolor*
Yambean. *See Pachyrhizus erosus*
Yambean, African. *See Sphenostylis stenocarpa*
Yam, Chinese. *See Dioscorea batatas*; *Dioscorea opposita*
Yam, Elephant. *See Amorphophallus campanulatus*
Yam, Korean. *See Dioscorea aimadoimo*
Yam, Lesser. *See Dioscorea esculenta*
Yam, White Guinea. *See Dioscorea rotundata*
Yam, Winged. *See Dioscorea alata*
Yam, Yellow Guinea. *See Dioscorea cayenensis*
Yassar. *See Moringa peregrina*
Yellowtops. *See Flaveria cronquistii*; *Flaveria pubescens*
Yellowtops, Brown's. *See Flaveria brownii*
Yellowtops, Clustered. *See Flaveria trinervia*
Yellowwood. *See Cladrastis lutea*
Yew, English. *See Taxus baccata*
Yew, Japanese. *See Taxus cuspidata*
Yew, Prince Albert. *See Saxegothaea conspicua*
*Yucca aloifolia* (Aloe Yucca), 413*t*
*Yucca flaccida* (Weak-Leaf Yucca), 18*t*, 42*t*, 312*t*, 392*t*, 469*t*

Yuko. *See Citrus yuko*
Yulan. *See Magnolia denudata*
Yuzu. *See Citrus junos*

**Z**

*Zantedeschia aethiopica* (Arum Lily), 89*t*, 223*t*
Zea mays (Corn, Maize), 7*t*, 18*t*, 33*t*, 42*t*, 59, 63*t*, 70*t*, 89*t*, 139*t*, 152*t*, 158*t*, 178*t*, 189*t*, 200*t*, 208*t*, 212*t*, 223*t*, 312*t*, 380*t*, 392*t*, 413*t*, 432*t*, 446*t*, 458*t*, 462*t*, 469*t*, 472*t*, 475–500
  ssp. *indentata* (Dent Corn), 223*t*, 490–500
  ssp. *indurata* (Flint Corn), 223*t*
  ssp. *saccharata* (Sweet Corn), 178*t*, 189*t*, 208*t*, 223*t*
*Zingiber officinale* (Ginger), 89*t*, 223*t*
*Ziziphus jujuba* (Jujube), 223*t*, 380*t*
Ziziphus vulgaris ssp. inermis
  ssp. *spinosus*, 380*t*
*Ziziphus vulgaris* ssp. *inermis*, 380*t*, 490–500
*Zostera asiatica*, 223*t*
*Zostera capricorni*, 223*t*
*Zostera marina* L. (Seawrack), 223*t*, 312*t*
*Zostera nana*, 223*t*
*Zygophyllum album* (White Bean Caper), 223*t*